Quaestiones

Entomologicae

A periodical record of entomological investigations,
published at the Department of Entomology,
University of Alberta, Edmonton, Canada.

CONTENTS

SYSTEMATICS OF THE GENUS GROUP TAXA OF THE SIPHONINI
(DIPTERA: TACHINIDAE)

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ABSTRACT

The Siphonini are a monophyletic tribe including 386 named species (including subspecies and nomina dubia, *but excluding* nomina nuda *and misspellings), of which 294 are recognized as taxonomically valid species. The genera and subgenera of the tribe are revised for the world fauna, based on study of adults of most described and more than 100 undescribed species, and first instars of 68 species. Seven genera are recognized, each hypothesized as monophyletic:* Goniocera *Brauer and Bergenstamm,* Proceromyia *Mesnil (elevated from subgeneric status within* Ceromya *and including* Nipponoceromyia *Mesnil and Shima, n. syn.),* Entomophaga *Lioy,* Ceromya *Robineau-Desvoidy (including new synonym* Actinactia *Townsend),* Actia *Robineau-Desvoidy,* Peribaea *Robineau-Desvoidy and* Siphona *Meigen.* Ceromya *is informally divided into* Ceromya sensu stricto *and the* Ceromya silacea *species group. The concept of* Siphona *is broadened to include the following nine subgenera, each previously recognized as a genus and each (except for one, as noted) hypothesized as monophyletic:* Actinocrocuta *Townsend (new subgeneric status),* Aphantorhapha *Townsend (new subgeneric status),* Aphantorhaphopsis *Townsend (new subgeneric status; an unresolved and possibly polyphyletic group of Old World species, including* Asiphona *Mesnil, n. syn.),* Baeomyia *O'Hara (new subgeneric status),* Ceranthia *Robineau-Desvoidy (new subgeneric status),* Pseudosiphona *Townsend (new subgeneric status),* Siphona *Meigen sensu stricto,* Siphonopsis *Townsend (new subgeneric status) and* Uruactia *Townsend (new subgeneric status). Three species groups, and a group of unrelated and unplaced species, of undescribed New World* Siphona s.l. *species are reviewed but not formally named or described.*

New combinations resulting from reclassification of the Siphonini are: Nipponoceromyia pubioculata *Mesnil and Shima moved to* Proceromyia; Actia amblycera *Aldrich,* Actia cornuta *Aldrich,* Actinactia lutea *Townsend and* Actia normula *Curran moved to* Ceromya; Actia stiglinae *Bezzi moved to* Peribaea; Actia panamensis *Curran and* Aphantorhapha pulla *Reinhard moved to* Siphona s.l. *(and unplaced to subgenus); and the following 20 species are provisionally placed in* S. *(Aphantorhaphopsis) (most formerly placed in* Asiphona, *a junior synonym of* S.

(Aphantorhaphopsis))*:* Crocuta (Siphona) alticola *Mesnil,* Actia angustifrons *Malloch,* Actia brunnescens *Villeneuve,* Crocuta (Siphona) crassulata *Mesnil,* Siphona (Asiphona) fera *Mesnil,* Siphona (Asiphona) laboriosa *Mesnil,* Actia laticornis *Malloch,* Actia mallochiana *Gardner,* Siphona (Asiphona) nigronitens *Mesnil,* Actia norma *Malloch,* Asiphona picturata *Mesnil,* Siphona (Asiphona) pudica *Mesnil,* Actia samarensis *Villeneuve,* Actia selangor *Malloch,* Thryptocera selecta *Pandellé,* Gymnopareia siphonoides *Strobl,* Siphona (Asiphona) speciosa *Mesnil,* Actia starkei *Mesnil,* Actia verralli *Wainwright and* Siphona (Asiphona) xanthosoma *Mesnil.* Actia heterochaeta *Bezzi, a* nomen dubium, *is left unplaced within the Siphonini. Removed from the Siphonini is* Actia aberrans *Malloch (referred to* Eurysthaea *Robineau-Desvoidy by Crosskey, pers. comm.).*

The status of named species has, in general, been maintained as listed in current literature, though the following new synonymies were recognized and are herein proposed: Actia brevis *Malloch synonymized with* A. darwini *Malloch,* Peribaea subaequalis *(Malloch) with* P. orbata *(Wiedemann),* Actinocrocuta chaetosa *Townsend with* Siphona (Actinocrocuta) singularis *(Wiedemann), and* Siphona janssensi *(Mesnil) with* S. (Siphona) cuthbertsoni *Curran. Elevated from subspecific to species status are:* Ceromya similata *Mesnil,* Siphona (Siphona) infuscata *(Mesnil) and* S. (Siphona) nigrohalterata *Mesnil. Lectotypes are designated for* Ceromya cibdela *(Villeneuve) and* S. (Pseudosiphona) brevirostris *Coquillett.*

A chapter about structural features of the Siphonini is followed by a key to genera and then by descriptions of genera and subgenera. Keys are also provided to the species of Proceromyia *and* Entomophaga *and for the subgenera of* Siphona s.l. *A list of known siphonine hosts is included. A cladistic analysis based on ingroup (Siphonini) and outgroup (other Tachinidae) comparisons is used to partially reconstruct the phylogenetic history of the major siphonine lineages. Geographic distribution of siphonine genera and subgenera is discussed in relation to historical events during earth history and the presumed phylogenetic history of the Siphonini.*

RÉSUMÉ

La Siphonini est une tribu monophylétique qui comprends 386 espèces nommées (y compris les sous-espèces et nomina dubia, *mais à l'exclusion de* nomina nuda *et ses mauvaises épelations). De ces espèces, 294 sont reconnues comme étant taxonomiquement valides. Les genres et sous-genres de la tribu sont revisés pour la faune mondiale, ce basé sur une étude des adultes de la plupart des espèces décrites, des adultes de plus de 100 espèces non- décrites, et des larves de premier stade de 68 espèces. On reconnait sept genres, et on hypothèse que chacun de ceux-ci est monophylétique:* Goniocera *Brauer et Bergenstamm,* Proceromyia *Mesnil (élevé du statu sous-genre dans* Ceromya *et y compris* Nipponoceromyia *Mesnil et Shima, n. syn.),* Entomophaga *Lioy,* Ceromya *Robineau-Desvoidy (y compris le nouveau synonyme* Actinactia *Townsend),* Actia *Robineau-Desvoidy,*

Peribaea *Robineau- Desvoidy et* Siphona *Meigen. A titre non-officiel,* Ceromya *est divisé en deux groupes:* Ceromya *sensu stricto et le groupe d'espèces* Ceromya *silacea. Le concept de* Siphona *est élargi pour inclure les neuf sous-genres suivants, chacun préalablement reconnu comme genre et chacun (à l'exception d'un tel, que noté) étant par hypothèse monophylétique:* Actinocrocuta *Townsend (nouveau statu sous-générique),* Aphantorhapha *Townsend (nouveau statu sous-générique),* Aphantorhaphopsis *Townsend (nouveau statu sous-générique; un groupe irrésolu et possiblement polyphylétique d'espèces de l'ancien monde, y compris* Asiphona *Mesnil, n. syn.),* Baeomyia *O'Hara (nouveau statu sous-générique),* Ceranthia *Robineau-Desvoidy (nouveau statu sous-générique),* Pseudosiphona *Townsend (nouveau statu sous-générique),* Siphona *Meigen sensu stricto,* Siphonopsis *Townsend (nouveau statu sous-générique). Trois groupes d'espèces, et un groupe d'espèces sans liens de parenté et d'espèces non-classèes, de* Siphona *s.l. du nouveau- monde sont examinés sans être nommes ou decrits formellement.*

Les nouvelles combinaisons résultant de la reclassification des Siphonini sont: Nipponoceromyia pubioculata *Mesnil et Shima passe à* Proceromyia; Actia amblycera *Aldrich,* Actia cornuta *Aldrich,* Actinactia lutea *Townsend et* Actia normula *Curran passent à* Ceromya; Actia stiglinae *Bezzi passe à* Peribaea; Actia panamensis *Curran et* Aphantorhapha pulla *Reinhard passe à* Siphona *s.l. (et non-classé au niveau du sous-genre); et les 20 espèces suivantes sont provisoirement placées dans S. (Aphantorhaphopsis) (plus antérieurement placées dans* Asiphona, *un synonyme junior de S. (Aphantorhaphopsis)):* Crocuta (Siphona) alticola *Mesnil,* Actia angustifrons *Malloch,* Actia brunnescens *Villeneuve,* Crocuta (Siphona) crassulata *Mesnil,* Siphona (Asiphona) fera *Mesnil,* Siphona (Asiphona) laboriosa *Mesnil,* Actia laticornis *Malloch,* Actia mallochiana *Gardner,* Siphona (Asiphona) nigronitens *Mesnil,* Actia norma *Malloch,* Asiphona picturata *Mesnil,* Siphona (Asiphona) pudica *Mesnil,* Actia samarensis *Villeneuve,* Actia selangor *Malloch,* Thryptocera selecta *Pandellé,* Gymnopareia siphonoides *Strobl,* Siphona (Asiphona) speciosa *Mesnil,* Actia starkei *Mesnil,* Actia verralli *Wainwright et* Siphona (Asiphona) xanthosoma *Mesnil.* Actia heterochaeta *Bezzi, un* nomen dubium, *demeure non-classé parmi les Siphonini.* Actia aberrans *Malloch est enlevé des Siphonini (et rapporté à* Eurysthaea *Robineau-Desvoidy par Crosskey, comm. pers.).*

*Le statu des espèces nomme*é*s a été maintenu en général, tel qu'inscrit dans la littérature, à l'exception des nouvelles synonymies reconnues et proposées comme suit:* Actia brevis *Malloch synonyme de A.* darwini *Malloch,* Peribaea subaequalis *(Malloch) synonyme de P.* orbata *(Wiedemann),* Actinocrocuta chaetosa *Townsend synonyme de* Siphona (Actinocrocuta) singularis *(Weidemann), et* Siphona janssensi *(Mesnil) synonyme de S. (Siphona)* cuthbertsoni *Curran. Les suivantes sont élevées de sous-espèces à espèces:* Ceromya similata *Mesnil,* Siphona (Siphona) infuscata *(Mesnil) et S. (Siphona)* nigrohalterata *Mesnil. Des lectotypes sont designes pour* Ceromya cibdela *(Villeneuve) et S. (Pseudosiphona)* brevirostris *Coquillett.*

Un chapêtre sur les traits structuraux des Siphonini est suivi d'une clef pour les genres, et ensuite par les descriptions des genres et sous-genres. Des clefs sont aussi incluses pour les espèces de Proceromyia *et* Entomophaga *et pour les sous-genres de* Siphona s.l. *Une liste des hôtes reconnus pour les siphonines est incluse. Une analyse cladistique basee sur des comparaisons en groupe (Siphonini) et hors groupe (autres Tachinidae) est utilisée pour reconstruire partiellement l'histoire phylogénétique des lignées majeurs siphonines. La distribution géographique des genres et sous-genres des siphonines est discutée en relation avec les évènements historiques de l'évolution de la terre, et l'histoire phylogénétique présomptueuse des Siphonini.*

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INTRODUCTION

The Siphonini are a monophyletic tribe of about 300 described species and more than 100 undescribed species, of uncertain phylogenetic position within the Tachinidae (some authors favoring its placement in the Goniinae, others the Tachininae). Adults are smaller than most tachinid flies, generally 3-5mm in length, and larvae are almost exclusively parasitoids of larval Lepidoptera. Siphonines are widely distributed throughout the world, with greatest diversity in non-rainforest areas of the tropics.

Mesnil established the modern concept of the Siphonini (as Siphonina) in his illustrious tachinid contribution to "Die Fliegen der palaearktischen Region" (1962-5). Prior to that time, several genera now relegated to the Neaerini were included because of their external similarity to members of the Siphonini (*e.g.* Mesnil 1939, 1954; van Emden, 1954). Herting (1957), in his interpretive survey of female genitalia in the Calyptratae, was first to recognize the error in this classification and his findings were subsequently incorporated into Mesnil's (1962-5) revision of the Palearctic Siphonini. Crosskey maintained Mesnil's concept of the tribe in his treatments of the tachinid faunas of the Australian (1973), Oriental (1976a) and Afrotropical (1980) regions, as did Andersen (1983) in his recent generic revision of the Old World Siphonini and Herting (1984) in his catalogue of Palearctic Tachinidae.

In marked contrast to the recent attention conferred upon Old World siphonines, the New World fauna is without a modern treatment at any level. Townsend's (1940) revision of the "Siphonini" and "Actiini" in his "Manual of Myiology" is an untenable classification comprising a heterogeneous and polyphyletic assemblage of genera. A valuable step toward a modern classification of North American Siphonini was achieved by Sabrosky and Arnaud (1965). These authors brought together almost all the siphonine taxa of America north of Mexico within their subtribe of the Siphonini, the Siphonina, but included therein a number of unrelated genera.

Guimarães (1971) catalogued the tachinids of America south of the United States, and though following the broad concept of the Siphonini advanced by Sabrosky and Arnaud, he did not similarly recognize subtribes; consequently his genera of the Siphonini *sensu* Mesnil are interspersed with a variety of unrelated taxa.

This study was undertaken with the aim of revising the supraspecific taxa of the Siphonini and in particular reclassifying the New World siphonines in light of recent advances concerning the Old World fauna. This aim has been tempered somewhat by the diverse and largely undescribed fauna of the Neotropics, which requires detailed study and description of species before a satisfactory supraspecific classification can be established. The results of a preliminary study of many undescribed Neotropical species are included here as an aid to future systematic research on the Neotropical Siphonini.

In addition to revising the Siphonini and providing a framework about which future revisions of genera can proceed, this work is also an exploration into the phylogenetic relationships among the supraspecific taxa and character state diversity among species. To attain this goal, most available types and specimens of many undescribed species were examined.

Included in this paper are lists of species names in the Siphonini, arranged according to a revised classification of the tribe. Descriptions of the genera and subgenera are provided along with keys to the genera of the Siphonini, subgenera of *Siphona s.l.* and species of *Proceromyia* and *Entomophaga*. Known hosts of the Siphonini are listed. Character state diversity is tabulated and discussed, and the phylogenetic and geographic history of the supraspecific taxa is analyzed.

MATERIALS AND METHODS

Materials

This paper is based on the morphological study of adult specimens of about 270 of the 294 described species of the Siphonini, more than 100 undescribed New World species, and numerous undescribed Old World species. Included among these specimens were 264 primary types and eight paratypes; types not examined include 31 known to be lost (22 of these being Robineau-Desvoidy nominal species) and 13 not located and possibly lost. Male genitalia of more than 250 species and female genitalia of about 90 species were examined. First instars of 68 species were also examined (see O'Hara in press "a").

Codes used in the text for designating institutions and private collections appear below with the names of their respective curators.

AMNH   Department of Entomology, American Museum of Natural
        History, Central Park West at 79th Street, New York, NY
        10024; the late P. Wygodzinsky and K.A. Schmidt.
BLKU   Biological Laboratory, College of General Education, Kyushu University,
        Ropponmatsu, Fukuoka 810, Japan; H. Shima.

BMNH Department of Entomology, British Museum (Natural History), Cromwell Road, London, England SW7 5BD; R.W. Crosskey and A.C. Pont.

BPBM Department of Entomology, Bernice P. Bishop Museum, P.O. Box 6037, Honolulu, HI 96818; N.L. Evenhuis.

CAS Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118; P.H. Arnaud, Jr.

CEA Colección de la Estación Experimental Agronómica, Universidad de Chile, Maipú, Chile (curator not named).

CIE Colección del Centro de Investigacions Entomológicas, Universidad de Chile, Santiago, Chile; J. Herrera.

CNC Biosystematics Research Centre [formerly Institute], Central Experimental Farm, K.W. Neatby Building, Ottawa, Ontario K1A 0C6; D.M. Wood.

DEI Institut für Pflanzenschutzforschung Kleinmachnow, [formerly the Deutsches Entomologisches Institut], Akademie der Landwirtschaftswissenschaften, Bereich Eberswalde, 13 Eberswalde-Finow 1, Schicklerstrasse 5, German Democratic Republic; H.J. Müller and R. Gaedike.

DPI Entomology Branch, Department of Primary Industries, Meiers Road, Indooroopilly, 4068, Queensland, Australia; B. Cantrell.

ETH Entomologisches Institut, Eidgenössische Technische Hochschule, Zentrum, CH-8092 Zurich, Switzerland; W. Sauter.

FRI Forest Research Institute, Dehra Dun, Uttar Pradesh, India. (I was unable to establish contact with this institution.)

FSF Forschungsinstitut Senckenberg, Senckenberganlage 25, D-6000 Frankfurt 1, Federal Republic of Germany; J. Rademacher.

HDE Hope Department of Entomology, University Museum, Oxford, OX1 3PW, England; M.J. Scoble.

HNHM Zoological Department, Hungarian Natural History Museum, H-1088 Budapest, Baross u. 13, Hungary; F. Mihályi.

INPA Instituto Nacional de Pesquisas da Amazônia, Caixa Postal 478, 69.000 Manaus, Amazonas, Brazil; J.A. Rafael.

IRSN Institut Royal des Sciences Naturelles de Belgique, Rue Vautier 31, B-1040 Bruxelles, Belgium (curator not named).

JEOH Private collection of the author.

MBR División Entomología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Avenida Angel Gallardo 470, Buenos Aires, Argentina; A.O. Bachmann.

MCSN Museo Civico di Storia Naturale, 20121 Milano, Corso Venezia 55, Italy; C. Leonardi.

MCZ Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138; M.K. Thayer.

MNHN Entomologie, Muséum National d'Historie Naturelle, 45 bis Rue Buffon, Paris Ve, France; L. Matile.

MRAC Entomology Section, Musée Royal de l'Afrique Centrale, B-1980, Tervuren, Belgium; E. De Coninck.

MSU Department of Entomology, Michigan State University, East Lansing, MI 48824; R.L. Fischer.

MZF Museo Zoologico de "La Specola", Università Degli Studi, Via Romana, 17-50125 Firenze, Italy; S. Mascherini.

NMBA Naturhistorisches Museum der Benediktiner-Abtei Admont, A-8911 Admont, Austria; B. Hubl.

NMV Entomology Department, Naturhistorisches Museum, Zoologische Abteilung, A-1014 Vienna, Burgring 7, Austria; R. Contreras-Lichtenberg.

NRS Entomology Section, Swedish Museum of Natural History, S-10405 Stockholm, Sweden; P.I. Persson.

OSU Department of Entomology, Oregon State University, Corvallis, OR 97331; M.D. Schwartz.

PHA Private collection of P.H. Arnaud, Jr., c/o CAS.

PPRI Department of Agriculture, Plant Protection Research Institute, National Collection of Insects, Private Bag X134, Pretoria 0001, Republic of South Africa; M.W. Mansell.

SMNS Staatl. Museum für Naturkunde, Rosenstein 1, D-7000 Stuttgart 1, Federal Republic of Germany; B. Herting.

SPHTM Entomology Section, School of Public Health and Tropical Medicine, Sydney University 2006, Sydney, New South Wales, Australia; M.L. Debenham.

UASM Department of Entomology, Strickland Museum, University of Alberta, Edmonton, Alberta T6G 2E3; G.E. Ball.

UAT Department of Entomology, University of Arizona, Tucson, AZ 85721; F.G. Werner.

UCB Division of Entomology and Parasitology, University of California, Berkeley 4, CA 94720; J.A. Chemsak.

UCD Department of Entomology, University of California, Davis, CA 95616; R.O. Schuster.

UCR Department of Entomology, University of California, Riverside, CA 92521; S.I. Frommer.

UCS Facultad de Agronomía, Universidad de Chile, Casilla 1004, Santiago, Chile; R. Cortés.

UKL Department of Entomology, Snow Entomology Museum, University of Kansas, Lawrence, KS 66045; C.D. Michener and G.W. Byers.

UNH Department of Entomology, University of New Hampshire, Durham, NH 03824; J.F. Burger.

UNLP   Division de Entomologia, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Paseo del Bosque, 1900 La Plata, Argentina; L. de Santis.

USNM   Systematic Entomology Laboratory, SEA, U.S. Department of Agriculture, United States National Museum, Washington, DC 20560; C.W. Sabrosky (retired) and N.E. Woodley.

USP   Museu de Zoologia, Universidade de São Paulo, Avenida Nazare, 481, Caixa Postal 7172, 04263, São Paulo, sp, Brazil; J.H. Guimarães.

UZI   Department of Zoology, Zoological Museum, Helgonavägen 3, S-223 62, Lund, Sweden; R. Danielsson.

WLD   Private collection of W.L. Downes, c/o MSU.

WSUP   Department of Entomology, James Entomological Collection, Washington State University, Pullman, WA 99164; W.J. Turner.

ZIL   Zoological Institute, USSR Academy of Sciences, Leningrad 199164, USSR; V.A. Richter.

ZMA   Instituut voor Taxonomische Zoölogie, Zoölogisch Museum, Universiteit van Amsterdam, Afdeling Entomologie, Plantage Middenlaan 64, 1018 DH Amsterdam, Netherlands; T. van Leeuwen.

ZMHU   Museum für Naturkunde an der Humboldt-Universität zu Berlin, Bereich Zoologisches Museum, DDR 104 Berlin, Invalidenstrasse 43, German Democratic Republic; H. Schumann.

ZMU   Division of Entomology, Zoological Museum of the University, SF-00100 Helsinki 10, Finland; B. Lindeberg.

ZMUC   Zoologisk Museum, Universitetsparken 15, DK 2100, Copenhagen, Denmark; S. Andersen.

Methods

Ranking of taxa.— Ideally a classification should be practical to the general taxonomist, informative to the specialist, and an accurate reflection of the hypothesized cladistic relationships among included taxa. In reality few groups can be so perfectly classified, as the three criteria are often to a greater or lesser extent at odds with one another. The problem is particularly acute when cladistic relationships are inadequately known, as in the Siphonini. In light of this problem, and in an effort to adhere as closely as possible to the three criteria given above, a classification for the Siphonini is proposed using the formal supraspecific categories of genus and subgenus and informal category of species group, with different criteria for each.

In addition to the accepted criterion of being phenetically distinct from one another (an admittedly vague concept), genera recognized herein are hypothesized as monophyletic (holophyletic) lineages which are distinguishable by non-genitalic characters (except for a few species possessing key-character parallelisms). Though in combination these criteria are still subjective, they are stated here simply to give

the reader some indication of the guidelines followed in erecting the Siphonini classification proposed herein; genera (like all taxa) are by nature subjective entities undefinable by objective criteria. Most significantly, the criteria used here have led to a broadening of *Siphona* to include a number of previously recognized genera (mostly of Townsend). This broadened concept of *Siphona* comprises a monophyletic group recognizable by the non-specialist; lower ranks within the genus are used (as explained below) to serve the needs of the specialist.

The rank of subgenus has been used sparingly during the taxonomic history of the Tachinidae, particularly by the most prolific describer of New World tachinids, C.H.T. Townsend. Townsend had a very restricted generic concept, generally erecting new genera of questionable value for the inclusion of a very few species. As Townsend's work is re-evaluated, most of his genera are being combined with others or his original generic limits expanded. With respect to the Siphonini, most of his genera proposed for non-*Siphona s.l.* species have been combined with other genera, leaving only his *Siphona* group genera, representing mostly New World taxa, unrevised. Whereas Townsend's genera previously combined with non-*Siphona* genera required no change to the concepts of those taxa, the same is not true of his *Siphona* group names. Each of these names (*i.e. Actinocrocuta, Aphantorhapha, Aphantorhaphopsis, Pseudosiphona, Siphonopsis* and *Uruactia*) designate lineages of unknown relationship to one another. Either they must all be retained as genera or the generic limits of another genus broadened for their inclusion, if one is to follow the criterion of monophyly stated above for genera. In addition, most of these lineages are phenetically similar, and only distinguishable by male genitalic characters. A compromise position has been adopted here by reducing Townsend's *Siphona* group genera to subgenera within a broadened concept of *Siphona. Siphona s.l.* is strictly monophyletic under this classificatory scheme, and lower units are given the equal rank of subgenus because of the unknown cladistic relationships among them. Thus such distinctive groups as *Baeomyia* and *Ceranthia* are also assigned subgeneric rank along with Townsend's names because their exclusion would make *Siphona s.l.* paraphyletic. By retaining Townsend's genera in a formal classification, albeit at lower rank, the taxonomic and phylogenetic unity of each of these taxa is retained, which would otherwise be lost if *Siphona* was broadened and no lower ranks recognized. Ideally, I would like to see some New World subgenera of *Siphona s.l.* combined with one another in the future, but at present no synapotypies are known upon which to base such action. More taxonomically and phylogenetically useful characters need to be discovered so that the numerous undescribed species of *Siphona s.l.* are not classified into new *Siphona* subgenera of unnecessarily narrow limits.

All *Siphona* subgenera are considered strictly monophyletic except one. An exception has been made for *S. (Aphantorhaphopsis)* on practical grounds. Old World species of the *Siphona* group not belonging to *Siphona s.s.* or *S. (Ceranthia)* have been assembled together in *S. (Aphantorhaphopsis)* as a preliminary measure

until the group can be adequately revised. Many of its described species are known only from holotypes - some male, others female - severely restricting their detailed study. Given also the rich undescribed fauna that belongs within this group, a revision of this assemblage is not attempted within this work. Preliminary study of these species suggests they have few, if any, close relationships with New World *Siphona s.l.* species, and almost certainly no close relationships with the New World *Siphona* subgenera recognized here.

The lowest supraspecific rank used is that of the informal species group. This rank is used for strictly monophyletic assemblages of species, and is used in two parts of the classification, once in *Ceromya s.l.* and again in *Siphona s.l.*

The species of *Ceromya s.l.* are arranged in *Ceromya s.s.* and the *C. silacea* species group, each tentatively hypothesized as monophyletic. This arrangement is presently incomplete because each can only be recognized by examination of male genitalia and not all species of *Ceromya s.l.* were examined for male genitalic states. The two groups of *Ceromya s.l.* are referred to as above to reflect the tentative nature of these findings and to avoid premature changes to the classification. If future studies support the monophyly of each group and their sister group relationship, then both could be formally recognized as subgenera of *Ceromya s.l.*

Nearly 100 undescribed siphonine species are known from the New World. More than half belong to such distinctive taxa as *Actia*, *Ceromya* and *Siphona s.s.*, or are included in the revised concepts of such *Siphona* subgenera as *Pseudosiphona* and *Siphonopsis*. The remainder do not exhibit clear relationships with any of the named taxa, although relationships are evident among some of these species. To reflect these relationships, document diversity, and to guide future studies on the assemblage, three numbered species groups are separately discussed, and the remaining 20-odd species treated as a whole. Thus the assemblage of known but undescribed species of New World *Siphona s.l.* is discussed in as detailed a manner as possible at this time. The naming of new species and possibly supraspecific taxa awaits a more detailed systematic examination of this diverse and undescribed fauna.

Treatment of undescribed species.— No new species is described in this work, though the characteristics of many are incorporated into the descriptions of the supraspecific taxa. I consecutively numbered (according to country or region of origin) undescribed species within each supraspecific taxon so that information obtained from these undescribed species could be usefully expressed herein. The examined specimens were appropriately labelled to permit their recognition in collections during future systematic studies of the Siphonini.

The numbering of undescribed species includes two or more higher taxa in two groups. The first involves *Ceromya s.l.*, in which undescribed species are numbered consecutively according to country or region of origin regardless of their placement in *Ceromya s.s.* or the *Ceromya silacea* species group. The second group involves species included in New World *Siphona* species groups 1 and 3 and unplaced

species of New World *Siphona s.l.*: these were numbered together consecutively from 1 to 34. [Groups 1 and 3 were recognized after the original numbering system was adopted, so their numbers were not changed when the species were shifted to their present classification. *Siphona* species group 2 was recognized before the other groups, and includes ten species numbered from one to ten.] One species from the above series, sp. 31, was recognized as near *S. (Uruactia) uruhuasi* and transferred to *S. (Uruactia)* without a change in number. Due to other taxonomic changes, no species in the *Siphona s.l.* series is numbered 9, 11 or 18 (*i.e.* these numbers are not used to designate undescribed species).

Terms.— Terms used here are those proposed by McAlpine (1981), with several changes as discussed in O'Hara (1983a: 269-70). Two additional changes are made with respect to male genitalia because of conflicting theories about genitalic homology. Griffiths' (1972, 1981) interpretation of homologies in male genitalia differs from that of McAlpine (1981), so the neutral terms pregonite and postgonite here replace McAlpine's controversial homology of these structures with, respectively, the gonopod and paramere. I also use the common terms epandrium and surstylus, though for descriptive purposes only and not in rejection of Griffiths' periandrial hypothesis about development of these structures.

The male abdominal sternum 5 is a sclerite of varied shape among siphonines. There do not appear to be standard terms available for detailed description of this structure, so I have chosen arbitrary terms for this purpose, and explain their meaning in the Structural Features chapter in characters 38 to 40. Features of this structure are labelled in Fig. 47.

Many terms used for head features, thoracic and abdominal setation, and genitalic structures are labelled in figs. 1-12 in O'Hara (1983a: 345-8); wing veins are labelled here in Fig. 21, features of first instars in Figs. 157-158, and varied external and genitalic features are labelled on scanning electron photomicrographs, Figs. 23-46.

Examination and illustration of specimens.— Adult specimens were examined with a Wild M5 stereoscopic microscope, with standard light source, at magnifications to 50X. Genitalia and first instars were studied with a Leitz SM-LUX compound microscope at magnifications to 400X. Though most genitalic features are visible at 50X with a dissecting microscope, there are certain taxonomically and phylogenetically important characters of the male genitalia, particularly those of the pregonite (characters 44-46), not readily discernible unless examined at 100X with a compound microscope or high resolution dissecting microscope (as discussed under appropriate characters in the Structural Features chapter).

Structures were drawn with the aid of a camera lucida or drawing tube, as explained in O'Hara (1983a: 268-9). Certain structures were gold-coated and examined and illustrated using a Cambridge M-250 scanning electron microscope. Illustrations referred to in other works are cited as "fig.", original illustrations shown

in this work are cited as "Fig.".

Genitalic dissections.— Male and female genitalia of siphonines provide some of the best character systems for taxonomic study and phylogenetic analysis. The genitalia of more than 600 siphonines were dissected during this study, following the method of O'Hara (1983a: 271-2). Briefly stated, this procedure involved removal of the abdomen from an adult specimen, partial clearing of the abdomen in 10% NaOH, dissection of genitalia, reattachment of abdomen to specimen, and storage of genitalia in glycerine. The abdomen generally changed little from its pre-dissection condition except for slight clearing and some shrivelling. Perhaps because of these minor changes, plus the time involved in preparation, most past workers have avoided study of siphonine genitalia despite the wealth of taxonomic and phylogenetic information they contain.

Genitalic preparations were stored during this study in short vials of glycerine in specially designed trays (O'Hara and McIntyre 1984), permitting direct examination and comparison among genitalia. Each dissection was numbered such that adult specimens and genitalia could be stored and examined separately and later easily re-associated. Genitalia were placed in microvials and pinned below their respective adult specimens for return of institutional loans. Dissection tags were placed in each microvial and attached to each pin to help prevent future accidental dissociation of genitalia and adult specimens, and to allow particular dissections referred to, or illustrated, herein to be identified in collections and restudied.

Each dissection was color-coded and numbered. The following colors were used, and a one letter abbreviation of each color identifies the appropriate dissection series in the text: blue (B), green (G), orange (O), red (R), white (W) and yellow (Y).

STRUCTURAL FEATURES

Historical review

The very long geniculate proboscis of *Siphona s.s.* species was recognized as a fundamental feature of that genus from the earliest writings about the Siphonini, but it was not until publication of Mesnil's (1954) work entitled "Genres *Actia* Robineau-Desvoidy et Voisins" that the concepts of other large siphonine genera reached their near-modern forms.

Mesnil (*op. cit.*) perceptively recognized the diagnostic value of two structural features of siphonines that had been noted by previous authors but not used at the generic level. One was Villeneuve's (1924: 22) discovery that the anal vein extended to the wing margin in certain species, which Mesnil used in the first couplet of his 1954 key (pp. 8-10) to distinguish *Strobliomyia* (=*Peribaea*), *Ceranthia*, *Siphona s.s.* and *Siphona (Asiphona)* (=*S. (Aphantorhaphopsis)*) from other siphonines. This state is now considered synaptypic of that group of taxa.

Mesnil (*op. cit.*) also recognized the generic value of Malloch's (1930b: 120) discovery that a group of species possesses a long, downwardly directed, lower proepimeral seta. Mesnil used this feature to differentiate *Strobliomyia* from other

genera in which the anal vein is extended to the wing margin, and to separate what are now considered neaerine genera from other siphonines.

Mesnil (*op. cit.*) further distinguished between two groups of genera based on basal setulation of wing vein R_{4+5}. In one group R_{4+5} was setulose from base to crossvein *r-m* or beyond, in the other only a single setula was present basally. Within the former group Mesnil keyed out *Goniocera* and established the modern concepts of *Actia* (as *Entomophaga*, as explained in O'Hara 1985) (based on the presence of a row of hairs on the katepisternum), and *Ceromya* (based on absence of this row of hairs). Mesnil's latter group was later transferred to the Neaerini by Herting (1957), based on study of female genitalia in the Calyptratae.

Mesnil synthesized the contribution of Herting (1957) into his revision of Palearctic tachinids in "Die Fliegen der palaearktischen Region" (1962-5). In that work Mesnil firmly established the modern concept of the Siphonini (as Siphonina), recognizing presence of a row of setulae on R_{4+5} as one of the fundamental features of the tribe. His generic classification, little changed from his 1954 publication, has become the touchstone of modern siphonine systematics.

Characterization of the Siphonini *sensu* Mesnil suffered from one shortcoming, namely the lack of a single feature which could be considered synapotypic of the tribe. Such was the situation when this work began in 1981. By then Crosskey (1973, 1976a, 1980) had revised the siphonine fauna of all Old World non-Palearctic regions, but the siphonine fauna of the New World was essentially unrevised and the applicability of Mesnil's tribal concept to the Neotropical fauna, in particular, was untested. At the suggestion of D.M. Wood, Biosystematics Research Centre, Ottawa, I investigated the possibility of two spermathecae in the female reproductive system being synapotypic of the Siphonini. All dissections of females during this study suggests that this state is synapotypic, and the same conclusion was reached independently by Andersen (1983). This fundamental feature of adult female siphonines is used here to define the world Siphonini and supplement former external characterization of the tribe based on Old World members.

Structural features of the Siphonini

The two major revisions of the Siphonini are those of Mesnil (1962-5) and Andersen (1983). Both are primarily based on the Palearctic fauna, and hence do not provide detailed information about the distribution of character states throughout the tribe. Such information is desirable not only to provide a sound phylogenetic basis for supraspecific concepts and descriptions (and an accurate key), but also as an aid to future revisers of siphonine taxa. Here follows an explanation of the characters used in the descriptions of the supraspecific taxa of the Siphonini, with designation of the states as they appear in Table 1. Table 1 is primarily intended as a quick reference to the distribution of character states within the Siphonini, both to summarize similarities and differences among supraspecific taxa and to augment the phylogenetic analyses of these taxa in the Evolution chapter.

Character 1. Length.— Adult siphonines are relatively small tachinids, ranging in total length from 2.0-6.5mm (as measured in profile from apex of flagellomere 1 in resting position to apex of abdominal tergum 5), with most species averaging between 3.0-5.0mm. Like most tachinids, adult siphonines vary intraspecifically in size, probably because of nutritional constraints placed upon them during their parasitic larval stage. It is thus not unusual to observe a considerable size range among conspecifics. This notwithstanding, the size of most individuals is closely grouped about the mean of that species, such that each species has a characteristic size. Ranges in total length given in Table 1 represent the size range observed among examined specimens of each taxon, and are rounded to the nearest 0.5mm.

Character 2. Proclinate orbital setae.— Two proclinate orbital setae are present on each side of the vertex of both male and female siphonines. Two states are recognized: one in which the anterior seta is longer than the posterior one (**A**), the other in which both setae are subequal in length (**S**). This character is not always useful taxonomically since some species possess both states and in others males and females differ (with the anterior seta larger in the female than in male in these species). There is also no evident trend toward one state or the other among the major siphonine lineages. In addition to the two states recognized here there is also marked variation, though difficult to quantify, in length and thickness of the proclinate orbital setae (particularly the anterior one) among siphonine lineages.

Character 3. Frontal setae.— Siphonines have a row of reclinate frontal setae which extend from about pedicel height to the anterior reclinate orbital seta. The frontal setae alternate short and long in all species except *Proceromyia pubioculata*, in which they are all long and unusually thin (Fig. 3). Also unique to *P. pubioculata* are 8-12 frontal setae, as other siphonines have no more than five (rarely six in atypical specimens). In many siphonines the fifth (uppermost) frontal is very short, and in a few lost altogether (often intraspecifically varied); a few species among different lineages characteristically possess only three frontal setae, though a series of specimens is needed to determine the stability of this state. The number of frontal setae in each taxon is listed in Table 1, and an asterisk beside a five is used to indicate that three or four frontals occur in some species (either characteristically or as an aberration).

Character 4. Eye vestiture.— Siphonines, as a rule, have bare (**B**) eyes (*i.e.* only a very few short and widely spaced hairs visible). The exception is *Proceromyia pubioculata*, which has a densely haired eye (**D**).

Character 5. Male eye height.— Eye size is markedly varied among siphonines, and as such is one of the most useful external characters for species recognition. Variation among species renders this character of little value at the generic level. In some lineages males and females of a species are apparently very similar in eye size, in other lineages the male or female may have the larger eye; this distinction was difficult to document with accuracy because of interspecific variation and because both male and female specimens of a species were not always available for

comparison. Therefore, I have made generalizations in the generic descriptions based on specimens available. Male eye size was selected as the standard for comparison among genera because males generally vary more in eye size interspecifically and possess the better characters for species identification (*i.e.* features of the male genitalia).

Overall eye size is difficult to measure, so eye height is used here for comparisons. Eye height is taken as the maximum vertical distance from top of eye to bottom, relative to vertical head height (excluding ocellar triangle; as in O'Hara 1983a). Some authors (*e.g.* Andersen 1982) measure eye height on a diagonal axis, resulting in slightly greater values than given here. Ranges in eye height are recorded in Table 1 and in descriptions; qualitative differences as well are given in the latter as an aid for comparisons, according to this arbitrary guide: small, eye up to 0.65 head height; medium-small, 0.66-0.69; medium, 0.70-0.76; medium-large, 0.77-0.84; and large, 0.85 and greater.

Character 6. Male flagellomere 1 length.— Characteristics of flagellomere 1 (termed third antennal segment by some authors), like eye size, are among the best external features by which to recognize species. One aspect that is easily quantified is that of flagellomere 1 length, as measured in profile from the suture on the pedicel to the most distant point apically, and expressed in relation to vertical head height (as in O'Hara 1983a). Male flagellomere 1 length has been used here for comparisons among genera because males of most species have the larger flagellomere 1 (*i.e.* longer and broader) and thus exhibit more interspecific variation in this character than females. As with eye height, a qualitative guide to flagellomere 1 length accompanies the numerical range given in descriptions, as an aid for comparisons among taxa. The following arbitrary length classes are used: short, less than 0.40 head height; medium-short, 0.41-0.48; medium, 0.49-0.60; medium-large, 0.61-0.69; and large, 0.70 and greater.

Character 7. Special modifications of male flagellomere 1.— Though the majority of siphonines possess an average shaped (*i.e.* not lobed) flagellomere 1, males (and only males) of a few species have unusual modifications, the functional significance of which is unknown. Included in this category are: bilobed flagellomere 1 (**B**; *e.g.* figs. 3a, 4a and 5a in Shima 1970a); trilobed flagellomere 1 (**T**; *e.g.* fig. 2a in Shima 1970a); and pectinate flagellomere 1 (**P**; *e.g.* Fig. 11, and fig. 1a in Shima 1970a). Absence of such modifications is indicated by an **A** in Table 1. The bilobed condition of male flagellomere 1 is found in a very few other tachinids besides the Siphonini (*e.g.* some species of the neaerine genus *Phytomyptera* Rondani), and a similar type of pectinate flagellomere 1 is found in males of *Borgmeiermyia* Townsend (figs. 1-5 in Arnaud 1963).

Character 8. Shape of male flagellomere 1.— Considered here is the general shape of male flagellomere 1, excluding the extreme modifications discussed under character 7. It is difficult to characterize flagellomere 1 shape into classes because its shape varies from one form to another in a continuous, non-graded manner. The

following states are broadly defined to cover the range of observed variation in shape of male flagellomere 1, and the cited figures illustrate examples of each. The states are: **L**, linear (Fig. 14); **A**, average (Fig. 17); **B**, broad (Fig. 6); **S**, subquadrangular (Fig. 15); and **T**, large and triangular.

Character 9. Aristomere 1 length.— The majority of siphonines have a short aristomere 1 (**S**), with a length half or less that of its width. Aristomere 1 is slightly elongate (**E**) - subequal in length and width - in a few species of several taxa. Most useful taxonomically and phylogenetically is state **L** (Figs. 4-5, 15), in which length of aristomere 1 is much greater than width (usually 2-4X longer than wide).

Character 10. Aristomere 2 length.— Aristomere 2 is elongate in siphonines and at least 1.5X longer than wide, with most species having an aristomere 2 in the range of 2-4X longer than wide. Length of aristomere 2 varies markedly within genera, and to a lesser degree even within some species, so this character is of limited taxonomic value above the species level. As a generalization, species with a very large flagellomere 1 also have a long aristomere 2, so there is some correlation in size between these structures in some lineages. Similarly, a long aristomere 2 generally accompanies a bilobed, trilobed or pectinate flagellomere 1. In Table 1 the range in size (length divided by width) of aristomere 2 is given for each taxon.

Character 11. Aristomere 3 length.— Aristomere 3 is varied in overall length and also in the degree to which it is tapered along its length; with length, and thickness along length, generally correlated. For this reason I have taken a subjective approach to this character rather than a strictly numerical one, using states that are visually interpretable. However, the difference between one state and another in the following series is subtle and the cited figures should be referred to as a guide for their discrimination. The states are: **V**, very short and either evenly tapered to tip or thickened to near tip (Fig. 15); **T**, short and thickened to near tip (Fig. 8); **S**, rather short and usually evenly tapered to tip (Figs. 10, 16; a very subjective interpretation of an aristomere 3 intermediate in form between **T** and the next state); and **L**, long and evenly tapered to fine tip (most figures, *e.g.* Figs. 6, 12, 18). Clear differences in shape and length of aristomere 3 among some lineages are useful both taxonomically and phylogenetically, even though intermediate states are difficult to categorize.

Character 12. Arista vestiture.— Amount of pubescence on the arista is constant within a few lineages and greatly varied in most. Lack of apparent pubescence is referred to as almost bare (**B**; most figures, *e.g.* Figs. 14-16). Other states form a graded series from micropubescent (**M**; Figs. 7, 20), pubescent (**P**; Figs. 10, 17), short plumose (**S**; Fig. 13), to medium plumose (**L**, long).

Character 13. Clypeus.— The clypeus is visible as a small sclerotized structure above the maxillary palpi when the proboscis is at least slightly extended. It is varied in form from narrow and partially enclosed laterally in membrane (**N**), to slightly (**S**) or distinctly broadened (**B**), to U-shaped (**U**).

Character 14. Maxillary palpus.— Most siphonines have a rather short, apically clavate palpus (**S**; most figures, *e.g.* Figs. 13-15). Particularly in species with an elongate proboscis, the palpus is correspondingly longer (**L**; Figs. 9, 20) and also apically clavate (*e.g. Siphona s.s.*). In *S. (Ceranthia)* species and two species of *S. (Aphantorhaphopsis)* the palpus is cylindrical (**C**; Fig. 16) along its length and varied in length from very short (reduced) to average.

Character 15. Prementum length.— Almost all species with padlike labella have a short (**S**; *e.g.* Figs. 1-2, 5-6) to medium length (**M**; *e.g.* Figs. 14, 18) prementum (*prem*). Species with elongate labella almost always have an elongate prementum (**E**; Figs. 9, 20) as well. I have not classed these states into discrete sizes, but as an approximate guide short is less than half head height, elongate approximates or exceeds head height, and medium is intermediate.

Character 16. Labella.— Of considerable taxonomic and phylogenetic importance is the length of the labella (*lbl*). The groundplan condition is padlike labella (**P**; *e.g.* Figs. 1-8), and this state is widely distributed throughout the Siphonini. A state common to many lineages but independently derived within most of them is slightly lengthened labella (**S**), which are slightly longer than wide. Less common are the following states: **M** (Figs. 13, 17), labella moderately lengthened and subequal to or slightly longer than half prementum length (characteristic of most *S. (Pseudosiphona)* species); **E** (Fig. 18), labella elongate and slightly shorter to slightly longer than three-quarters prementum length (typical of most *S. (Siphonopsis)* species); and **L** (Figs. 9, 20), labella as long as or longer than prementum (all *Siphona s.s.* species and a few species in other lineages).

Character 17. Prosternum.— The prosternum of most siphonine species is setulose (**S**), generally with a single pair of setulae but in a few species with several pair. A bare prosternum (**B**) is characteristic of a few species, though more commonly a bare specimen belongs to a species in which the prosternum is typically setulose.

Character 18. Lower proepimeral seta.— All siphonines have a strong, upturned seta (*u prepm s*) on the lower portion of the proepimeron. In addition, a strong lower seta (*l prepm s*) is present and directed downward in *Peribaea* (state **P**; Fig. 27). In other taxa the lower proepimeral seta (prostigmatic seta of some authors) is hair-like or absent (**A**; Fig. 28).

Character 19. Anepisternum.— The upper region of the anepisternum has a patch of hairs and one to three larger setulae (*anepst s*), as recorded in Table 1 (one large setula shown in Fig. 32, two in Fig. 31). In most species the number of setulae is apparently constant, in others varied; as well, in certain genera there is a characteristic number of setulae while in others the number is varied.

Character 20. Katepisternum anterior to mid coxa.— The katepisternum is considered bare (**B**) anterior to the mid coxa if several hairs are present along (and restricted to) the lower portion adjacent to the ventral midline (Fig. 34). In most *Actia* species and *Entomophaga exoleta* a row of hairs (*kepst h*) extend upward

anterior to the mid coxa from the ventral midline almost to the lower katepisternal seta (**S**; Fig. 33).

Character 21. Lower katepisternal seta.— Three setae are in a triangular arrangement on the upper portion of the katepisternum. The lower seta (*l kepst s*) is varied in length, and compared with the upper anterior seta is shorter (**S**; Fig. 31), approximately equal in length (**E**), or distinctly longer (**L**; Fig. 32 [seta appearing equal in length to upper anterior seta due to perspective]).

Character 22. Postsutural dorsocentral setae.— Three or four postsutural dorsocentral setae are present, as indicated in Table 1. As a generalization, the setae are longer and thicker (*i.e.* stronger) in species with three postsutural dorsocentrals than in those with four. Though the states of this character are constant within some species and lineages, they vary within a few species (*e.g.* several species of *Siphona s.s.*).

Character 23. Preapical anterodorsal seta on fore tibia.— This seta is varied from apparently absent to long. As compared with the preapical dorsal (*d*) seta on the fore tibia, it is either shorter (**S**) or approximately equal in length or longer (**E**).

Character 24. Anterodorsal seta on mid tibia.— Most siphonines possess one strong anterodorsal seta (*ad s*) on the lower half of the mid tibia (Fig. 37). This seta is lacking from *S. (Baeomyia)* species (Fig. 38) and several species of *Actia*, and a row of *ad* setae is present in *Goniocera*. Number of *ad* setae present on the mid tibia is shown in Table 1.

Character 25. Tarsomere 5 modification.— An average (**A**) tarsus is common to the groundplan of the Siphonini. One to several species in separate lineages possess a modification in tarsomere 5 of females (not known in males). Tarsomere 5 is enlarged in these species - broader and longer than in other siphonines (*e.g.* fig. 22 in Richter 1980 [female mislabelled as male]) and in most species with a dense patch of sensory hairs ventrally. This specialization is restricted to the fore leg in most species (**F**), but is present on all legs in a very few (**L**).

Character 26. Tarsal claw length.— Claws and pulvilli are short in most siphonines (**S**; *e.g.* figs. 4 and 6 in O'Hara 1983a). In a few species the claws are large (**L**; *e.g.* fig. 5, *op. cit.*), and generally larger in males than females. **M** designates a medium or intermediate-sized tarsal claw.

Character 27. Wing vein R_1 dorsally.— Setulation of vein R_1 dorsally can be discretely divided into three states: **B**, bare (Fig. 22); **D**, setulose distally; and **E**, setulose along its entire length (Fig. 21). Species do not vary between states **D** and **E**, though many species vary between **B** and possessing one to several setulae distally near the costal margin.

Character 28. Wing vein R_1 ventrally.— Vein R_1 ventrally is either bare (**B**) or distally setulose (**D**). As with character 27, some species vary between state **B** and possessing one to several setulae distally near the costal margin.

Character 29. Wing vein R_{4+5} dorsally.— Setulation of vein R_{4+5} is the most useful wing character taxonomically other than character 33. It is setulose (with four

to many setulae) in all siphonines and is one of the diagnostic features of the tribe. Two states are recognized, and only a very few species vary between one state and the other: **P** (proximal), R_{4+5} setulose between base (bifurcation of R_{2+3} and R_{4+5}) and crossvein *r-m* (Fig. 22); and **E**, R_{4+5} setulose from base to beyond crossvein *r-m* (Fig. 21).

Character 30. Wing vein CuA_1 dorsally.— Most siphonines have either a bare (**B**; Fig. 21) or partially setulose vein CuA_1. This vein is either setulose from crossvein *bm-cu* outward (**S**; Fig. 22), or in a very few species is additionally setulose proximal to *bm-cu* (**P**). State **P** is constant in those species with that state, but a few species vary between state **B** and possessing several setulae on CuA_1 (a <u>row</u> of setulae on CuA_1 is a good species-constant state).

Character 31. Setulation of other wing veins.— Setulation described in characters 27-30 are average for the Siphonini (**A**). Setulation on normally bare veins is noted here for several species: **B**, *Ceromya* Brazil sp. 5, with veins *Sc* and R_{2+3} setulose ventrally; **C**, *Actia ciligera*, with veins R_{2+3}, R_{4+5} and *M* setulose dorsally and ventrally; **F**, *Actia fallax*, with vein *M* setulose ventrally; **M**, *Peribaea modesta*, with vein R_{2+3} setulose dorsally and ventrally; and **S**, some specimens of the *S. (Actinocrocuta) singularis* complex, with vein *Sc* setulose ventrally.

Character 32. Loss of vein M distally.— Vein *M* is complete (**C**; *i.e.* extended to wing margin) in the majority of siphonines; in some species of *Actia* (involving several species groups) it fades out before its characteristic bend towards the wing tip in the apical one-fourth of wing (**N**). In a few *Actia* species the bend of *M* is faint but still visible.

Character 33. Anal vein.— This is one of the most significant characters in the Siphonini. The anal vein either fades out before the wing margin (**N**; Fig. 21) or is extended to the wing margin at least as a fold (**E**; Fig. 22). The latter state is rare in other tachinids, and of great diagnostic and phylogenetic importance in the Siphonini.

Character 34. Position of crossvein dm-cu.— The position of crossvein *dm-cu* is varied from near wing margin (Fig. 21) to relatively far removed from it (Fig. 22). A measure of *dm-cu* position was obtained by dividing the distal length of CuA_1 (distance from *dm-cu* to wing margin) by proximal length of CuA_1 (distance from crossvein *bm-cu* to *dm-cu*). The range in values for each taxon is given in Table 1 along with the number of species examined (generally one specimen measured per species), the mean, and standard deviation (SD). This character is discussed in detail in O'Hara (in press "b").

Character 35. Median marginal setae on abdominal terga 1+2.— Median marginal setae are considered absent (**A**) from abdominal terga 1+2 (T_{1+2}) if they cannot be distinguished from adjacent setulae. If they are slightly longer and thicker than adjacent setulae then they are considered weak (**W**), and if subequal in size to the median and lateral marginals on T_3 they are strong (**S**) (states **A** and **S** are illustrated in figs. 7-8, O'Hara 1983a). Some species with state **S** are constant for

this state, while in other species all states are present among different individuals or some specimens have a strong median marginal on one side and lack one on the other.

Character 36. Lateral marginal setae on abdominal terga 1+2.— States **A** (absent), **W** (weak) and **S** (strong) are the same as described for character 35 (see figs. 7-8 in O'Hara 1983a for states **W** and **S**). This character varies intraspecifically as in character 35, though generally such variation is between states **A** and **W**; most species with strong lateral marginal setae (**S**) rarely vary from this state.

Character 37. Setation on abdominal terga 3 to 5.— The average condition (**A**) is one in which tergum 3 (T_3) has a pair of strong median and lateral marginal setae and tergum 4 (T_4) and tergum 5 (T_5) each have an evenly spaced row of six marginal setae (figs. 7-8 in O'Hara 1983a). Additionally, in some species T_3-T_5 have weak to strong lateral discal setae (**D**) and/or an extra pair of lateral marginal setae (**L**).

Character 38. Posterior processes of male abdominal sternum 5.— Male sternum 5 (S_5) consists of an anterior (basal) plate (*bs p*) and two posterior processes. The processes are separated from one another by a median cleft (*med c*) and bordered anteromedially by a broad desclerotized area (*descl a*) of varied size (Fig. 47). Shape of the processes is greatly varied, but two general areas are recognized on each process: the apical lobe (*ap l*) and median lobe (*med l*) (Fig. 47). In most *Actia* species the median lobes are undifferentiated and the apical lobes are long and broadly continuous with the processes, resulting in a more or less V-shaped S_5 (**A**, *Actia*-type; Figs. 58-59). In a few other siphonines S_5 resembles the **A** state of *Actia* except the median lobes are distinctly differentiated and partially enclose the median cleft (**V**; Figs. 61, 64). In most siphonines the apical lobe is more narrowed preapically, and in combination with a distinctly differentiated median lobe produces a sharply or broadly defined U-shaped posterior margin (**U**; *e.g.* Figs. 47, 50, 65-70) or one in which the angle between apical and median lobes is obtusely angled (**O**; *i.e.* an intermediate state between V-shaped and U-shaped, *e.g.* Figs. 48-49, 60). A few siphonines have an undifferentiated apical lobe and rounded median lobe, producing a more or less transverse sternal margin posteriorly (**T**; Figs. 51-52, 57).

Character 39. Apical lobe of male abdominal sternum 5.— Within lineages possessing a preapically narrowed apical lobe and U-shaped S_5 posteriorly (see character 38), there is a trend toward curving inward (*i.e.* medially) of the apex of the apical lobe. State **A** designates the average condition in which the apical lobe is directed posteriorly (*e.g.* Figs. 47, 50, 66-68); **C**, an apical lobe distinctly curved inward (Figs. 56, 62-63, 65, 69); and **S**, an intermediate state in which apical lobe is slightly curved inward (Figs. 53-54).

Character 40. Median lobe of male abdominal sternum 5.— This feature of considerable variation is here defined as the region bordering the median cleft posteriorly, and continuous with the posterior process laterally. It is undifferentiated (**U**) in those species of *Actia* in which the sternal margin posteriorly is V-shaped and

median cleft not bordered by lobes (Fig. 58). In the simplest developed form the median lobe is rounded along its median margin (**R**) and partially encloses the median cleft (*e.g.* Figs. 55, 64, 67). In more developed forms the median lobe is truncate (**T**; *e.g.* Figs. 63, 66) along its medial or posteromedial margin or very broad and longitudinally elongate (**E**; *e.g.* Figs. 53, 69). In *Goniocera* species and a few other species the median lobe forms a broad, truncated plate flattened in a more or less posteromedial plane (**F**; Figs. 47, 54). State **F** is a highly derived form of median lobe, and between it and state **T** are a range of intermediates here classed as state **I**, characterized by a truncate margin and rather flattened surface posteromedially (Fig. 68). Some species, particularly within *Siphona s.l.*, have an accessory lobe on the median lobe posteriorly (**A**; Fig. 70).

Character 41. Setulation of male abdominal sternum 5.— Sternum 5 is bare on the basal plate, anterior to the desclerotized area. The posterior processes are sparsely (**S**), moderately (**M**), or densely (**D**) setulose. The processes may also have one pair of setae distinctly larger than the surrounding setulae, but presence or absence of these setae has been interpreted as too intraspecifically varied to be usefully characterized here.

Character 42. Size of male abdominal tergum 6.— Male tergum 6 (T_6) is separated from the epandrium by a narrow strip of membrane. In a few siphonines T_6 is unsclerotized (**A**, apparently absent), while in most it is varied from tiny to small lateral sclerites (**S**), to larger lateral sclerites (**L**), to a narrow to broad dorsally continuous sclerite (**D**).

Character 43. Width of ejaculatory apodeme.— The ejaculatory apodeme in the male genitalia has a bulbous base and a fan-shaped apical portion of varied size. Width of the fan-shaped portion is expressed herein as a function of the preapical width of the hypandrial apodeme (as measured dorsally). The relative width of the fan-shaped portion is given either as a measured range or expressed in relative terms in Table 1 and descriptions. The following states of the latter are recognized: **N**, ejaculatory apodeme slightly narrower than hypandrial apodeme; **S**, apodemes subequal in width; and **W**, ejaculatory apodeme slightly wider than hypandrial apodeme.

Character 44. Shape of pregonite.— Pregonites are structures to either side of the aedeagus, articulated at their bases with the hypandrium. A thin membrane extends anteriorly from the apex of each pregonite to the ventral surface of hypandrium. Pregonite shape is varied in many and subtle ways and cannot be classified into states without grouping similar forms in a subjective manner. I have tried to select and describe states I perceive as most meaningful in a taxonomic and phylogenetic sense, though it must be noted that even a continuous transformation series cannot be hypothesized since most states could easily have been derived from one of several others. The following states are recognized, and are arranged alphabetically because of the complexity of this character: **A**, average, smoothly curved along posterior margin or bent rather sharply at midlength, and pointed or

rounded apically (Figs. 73-76, 89-94, 96-106); **C**, C-shaped (open side facing anteriorly) and broad at midlength (Figs. 87-88); **F**, fused basally with hypandrial apodeme (only observed in *S. (Aphantorhaphopsis) nigronitens*); **J**, broad subapically and more or less J-shaped (Figs. 85-86); **L**, linear and only slightly curved apically (Fig. 72); **M**, anterior membranous portion enlarged, apex of pregonite generally not curved anteriorly (Figs. 77, 79-81); **O**, ring-shaped (Fig. 78), though part of ring incomplete in a few species; **P**, elongate and curved posteriorly (unique to *Ceromya lutea*, Fig. 83); **S**, thin and sickle-like, with basal arm slightly extended anteriorly (Fig. 84); **T**, basally broad and apically truncate (Fig. 71); and **W**, broadened or wide along most of length, with short pointed apex (Fig. 95).

Character 45. Pregonite modifications.— The pregonite has a smooth outer surface in the groundplan condition. Spines (*sp*) or spinules (*spin*) adorn the pregonite in a number of genera, and the size, pattern and location of these are classed into discrete, non-continuous states. However, not all of the following states can be seen with a dissecting microscope (at 50X), so it is necessary to examine the pregonite at a power of 100X or more with a compound microscope to discern with certainty whether small spinules are present or absent (**A**; *e.g.* Figs. 72, 76, 84, 87-88, 90-94). The spinose states are: **L**, longitudinal ridge on anterolateral surface with spines in single row along edge (Figs. 73-75, 103-105); **M**, anterior membranous portion (*memb p*) of pregonite expanded, usually with field of spinules on lower portion (Figs. 39-40, 71, 83, 79-81; these spinules are too small to be seen with most dissecting microscopes in specimens of most species); **E**, similar to state **M**, but in addition has laterally directed spines on anterolateral portion of sclerotized area (Fig. 82); **R**, ring-shaped pregonite (state **O** in character 44) with spinules anteriorly (Fig. 78); **S**, sclerotized portion (*scl p*) of pregonite with field of spines distally, with largest spines along apical margin (Figs. 41-42, 85-86); and **T**, sclerotized portion of pregonite with field of tiny spinules distally (Figs. 89, 95, 100; as with state **M**, these spinules are very small in specimens of some species, and not readily discernible with most dissecting microscopes).

Character 46. Posterior seta on pregonite.— Some members of *Siphona s.l.* possess a tiny to long seta at about midlength on the posterior surface of the pregonite. Different setal size classes are recognized because certain lineages possess a seta with a characteristic length. However, setal length is varied among some species, and varied between absent and small to medium in a few. Given the varied nature of this character, the following imprecisely specified states are recognized: **A**, absent (*e.g.* Figs. 71-82); **T**, very tiny seta (Figs. 89, 93, 97-98, 103-104, 106; not readily discernible without aid of a compound microscope); **M**, short to medium-sized seta (Figs. 90-92); **L**, long, thick seta (Fig. 94; as characteristically present in species of *S. (Ceranthia)*); and **F**, two to a few tiny to short setae (Fig. 95).

Character 47. Epiphallus.— An epiphallus is a subbasal, posterior outgrowth of the aedeagus. A small epiphallus is best seen in dorsal or ventral view, where

unobstructed by epandrium or postgonite. The following states are recognized: **A**, absent; **S**, small (short); **N**, relatively large but narrow; and **P** (present), relatively large and average width.

Character 48. Posterior margin of distiphallus.— The distiphallus is a cylindrical structure of varied size, shape and sclerotization. Several characteristics of the distiphallus appear to be more or less independent of one another, and three are considered here as characters 48 to 50. Character 48 describes the relative amount of sclerotization along the posterior margin of the distiphallus. The posterior margin is either entirely sclerotized to near apical margin of distiphallus (**E**; *pos marg* in Fig. 116), or is incised or desclerotized to varied degrees (**I**). The latter state can be recognized in lateral view in most species of *Siphona s.l.* by the presence of a pointed, sclerotized projection on the distiphallus posteriorly, below the narrowed attachment of basiphallus and distiphallus (*e.g. scl proj* in Figs. 125, 127).

Character 49. Posterolateral margin of distiphallus.— The lateral surfaces of the distiphallus, as viewed in profile, provide among the best features for species separation and recognition within the Siphonini. Shape of the distiphallus is too varied to be fully categorized at the generic level, but two aspects have been selected for description as characters 49 and 50. Character 49 refers to the posterolateral margin (apically) of the distiphallus. In some siphonines it is reduced (*r lat marg* in Fig. 108) or not differentiated (*i.e.* not incised; *undif pslat marg* in Fig. 124) from the rest of the distiphallus (**A**; *e.g.* Figs. 108-111, 115-124). In other siphonines the posterolateral margin of the distiphallus is incised from the rest of the lateral margin and slightly to markedly elongate, mostly independently among different lineages. This is a difficult character to classify into states, though the following series gives a rough indication of the diversity of this character among the recognized siphonine lineages: **S**, posterolateral margin separated from lateral margin by narrow incision and not extended beyond apex of lateral margin (present in *Goniocera io*, but not visible in Fig. 107 because posterolateral margins are curved inward); **M**, moderate apical extension of posterolateral margin beyond rest of lateral margin (*m pslat marg* in Fig. 125) and usually pointed or spined (either continuous with lateral margin or incised from it; Figs. 125, 131, 134); and **E**, as in state **M** but apically extended well beyond apex of rest of distiphallus (*l pslat marg* in Figs. 112 and 127) (Figs. 112, 114, 127, 133, 136).

Character 50. Spines on lateral margin of distiphallus.— The lateral and anterolateral surfaces of the distiphallus are adorned with small spinules, especially conspicuous anteriorly and apically. In some siphonines no larger spines are present (**A**; Figs. 107, 115-118, 132-135), in others the lateral margins are armed with conspicuously larger, usually recurved, spines along anterior and/or apical margin (**P**; Figs. 108-111, 114, 121, 124, 128). The degree to which these spines are differentiated is very useful taxonomically, particularly at the species level, but is too varied to be categorized here.

Character 51. Postgonite size.— Paired postgonites extend posteriorly from either side of the aedeagus basally. They are large (**W**, well developed) and conspicuous in most siphonines. Postgonites are short (**S**) in some siphonines (about as long as width of basiphallus subbasally), or reduced (**R**) to scarcely discernible lobes at base of basiphallus.

Character 52. Surstylus basally.— Each surstylus articulates basally with the epandrium and cerci. In most siphonines it is attached membranously (**M**; Figs. 139-144), in a few there is a narrow sclerotized connection between the epandrium posteriorly and surstylus basally (**F**, epandrium and surstylus fused; Figs. 137-138).

Character 53. Shape of surstylus.— The average condition (**A**) of the surstylus, as viewed in profile, is one in which it is narrowed at about midlength and either straight or slightly curved posteriorly near apex (Fig. 141). The following states are qualitative departures from the average condition (see cited figures for examples): **S**, short (Fig. 142); **B**, distinctly broader than average (Fig. 138); **C**, markedly curved posteriorly (Fig. 139); and **L**, elongate (Fig. 137).

Character 54. Shape of male cerci.— The cerci of siphonines are fused medially and tapered to a single slender apex. Their shape is described in lateral view, with average (**A**) being slender on lower half, smoothly curved at midlength and curved anteriorly near apex (Fig. 141). The following shapes are recognized, relative to the average shape: **S**, short (Fig. 138); **B**, broadened; **E**, elongate (Fig. 140); **L**, linear or straight along posterior margin in profile; **R**, same as state **L** but short (Fig. 139); and **I**, sharply inflexed at midlength, short to long in length (Figs. 137-138, 140; state **I** may be accompanied by one of the former states).

Character 55. Female ovipositor length.— The ovipositor, or female genitalia, is primitively short and only slightly extensible. More extensible ovipositors have evolved independently within different lineages, perhaps as an adaptation for depositing larvae directly upon hosts (as suggested by Andersen 1983). Extensible ovipositors are telescopic and characterized by broad regions of intersegmental membrane, and often elongated sclerites as well. Degree of extensibility is classed as follows: **S**, short and only slightly extensible (Figs. 43-46, 146-148, 151-153); **M**, moderately extensible (Figs. 145, 149-150, 154); **E**, elongate (Fig. 155); and **V**, very elongate (Fig. 156).

Character 56. Shape of female sternum 6.— The most apparent modifications to the female genitalia, other than extensibility, involve shape of sterna 6 (S_6) and 7 (S_7). Modification of S_6 is not common among siphonines, and is apparently always accompanied by similar or more pronounced modification of S_7. In the average (**A**) condition S_6 is slightly rounded on its ventral surface (Figs. 43-46, 145-153). Several types of modification are recognized: **W**, weakly or slightly keeled (*kl*) posteromedially; **S**, sharply keeled posteromedially (Fig. 154); **M**, moderately elongate (Figs. 154, 156); and **E**, elongate (Fig. 155).

Character 57. Size of female tergum 6.— Female tergum 6 (T_6) is varied in size as follows: **A**, absent; **S**, very small lateral sclerites (Fig. 152); **L**, moderate-sized

lateral sclerites (Figs. 145, 148, 151, 155-156); **M**, dorsomedian sclerite, not extended laterally; **D**, single sclerite extended dorsally and laterally (Figs. 153-154); and **N**, as in state **D** but narrowly discontinuous dorsally (Figs. 146-147, 149-150).

Character 58. Anterior apodeme on female sternum 7.— Female sternum 7 (S_7) is without an anterior apodeme (**A**, absent) if its anterior margin is broadly rounded (Figs. 145, 149, 151-156). An apodeme is present if a sclerotized arm extends anteriorly from the anteromedian margin of S_7, and is classed as either short (**S**; Fig. 150) or long (**W**, well developed; Figs. 146-148, *ant apod* in Fig. 147).

Character 59. Shape of female sternum 7.— As mentioned under character 56, modifications to sterna 6 (S_6) and 7 (S_7) are the most conspicuous in female genitalia other than extensibility. The following states are similar to those given for character 56: **A**, average condition, S_7 slightly rounded ventrally (Figs. 43, 45, 145-146, 148-153); **W**, weakly or slightly keeled (*kl*) posteromedially (Fig. 147); **S**, sharply keeled posteromedially (Figs. 44, 46); **E**, elongate (Figs. 155-156); and **L**, elongate and keeled posteromedially (Fig. 154).

Character 60. Size of female tergum 7.— Female tergum 7 (T_7) is varied in size as follows: **A**, absent; **S**, very small lateral sclerites (Figs. 151-152); **L**, moderate-sized lateral sclerites (Figs. 145-150, 153); and **F**, lateral sclerites fused with S_7 (Figs. 154-156).

Character 61. Location of spiracle of segment 7.— The position of the spiracle of segment 7 is varied. In some siphonines it is located in segment 7, close to or in T_7 or dorsal to margin of S_7 (state **P**, posterior; Figs. 148, 153-156). In other siphonines the spiracle is located dorsolaterally in membrane between segments 6 and 7 (state **I**, intermediate; Figs. 145, 150-152) or anteriorly in segment 6 in or near T_6 (state **A**, anterior; Figs. 146-147, 149).

Character 62. Characteristics of female sternum 8.— Female sternum 8 (S_8) is varied in several ways. In the average (**A**) condition it is a small sclerotized plate partially covered by S_7, and sparsely haired posteriorly (Figs. 43-46, 146, 148-153; average condition but bare in *Peribaea* species). Other states are as follows: **L**, lacking or absent (Figs. 147, 154-156); **R**, reduced in size (Fig. 145); **W**, much wider than average; **B**, bare or almost so; and **S**, with thick setae posteriorly (setation not shown in figures).

Character 63. Size of female tergum 10.— Tergum 10 (T_{10}) is located dorsal to the cerci (*cer*). It is small and sparsely haired in most siphonines, and present as either a median sclerite (**M**) or as two slightly separated sclerites (**P**, paired; a few species possess both·states). In a few siphonines T_{10} is unsclerotized (**A**, absent) or reduced in size (**R**).

Character 64. Labrum of first instar.— The anterior end of the cephalopharyngeal skeleton of first instars of the Tachinidae is extended forward between the lateral sclerites, and is tentatively homologized with the labrum by Wood (1987: 1196) (often termed "mouth hook" by previous authors). As in other tachinids, the labrum of first instar siphonines varies from hook-like (**N**, narrow in

dorsal-ventral plane; Figs. 159, 161-162) to hatchet-like (**B**, broadened in dorsal-ventral plane; Figs. 158, 160, 163). In a few siphonines the labrum is intermediate between these states, and here termed slightly broadened (**I**). First instars of the Siphonini are described by O'Hara (in press "a").

Character 65. Dorsal cornu of cephalopharyngeal skeleton of first instars.— In most larval siphonines and other larval tachinids there are two cornua posteriorly on the cephalopharyngeal skeleton, one dorsal (*d corn*) and one ventral (*v corn*) (**P**; Figs. 158-159, 161-163). The dorsal cornu is absent (**A**) from all nine *Actia* species examined for this character (Figs. 160). The possible presence of a dorsal cornu in *Actia dubitata*, illustrated in Farinets (1980), is indicated by a "?P[1]" in Table 1.

Character 66. Posteroventral margin of abdominal segment 6 of first instars.— First instars of the Siphonini are equipped with spinules or hooks externally. The greatest modification and variation in these structures are found on the last several abdominal segments, particularly the posteroventral margin of segments 6 and 7. Segment 6 is bare or has small spinules (**B**) posteroventrally (Figs. 157-161), or large spinules to hooks. If large spinules or hooks are present (Figs. 162-163), then their number is entered in Table 1.

Character 67. Posteroventral margin of abdominal segment 7 of first instars.— Segment 7 possesses ventrally a row or rows of spinules along its posterior margin, anterior to the anus. Two states are recognized: **R**, two or more even or uneven rows of spinules (Figs. 157-162); and **S**, a single dominant row of spinules (Fig. 163).

Table 1. Distribution of character states in the Siphonini. Refer to text for explanation of characters and states. (Superscripts indicate the number of species possessing a state, an asterisk denotes a state shared by most species in a taxon, an arrow signifies the presence of states intermediate to those on either side of arrow, and a diagonal slash (/) indicates that two states are present in the single examined species of that taxon.)

Character	1	2	3	4	5	6	7	8	9	10	11	12
						Male flagellomere one			Aristomere length			Arista
Taxon	Length (mm)	Proclinate orbitals	Frontal setae	Eye vestiture	Eye height	length	modification	shape	1	2	3	vestiture
Gonlocera	4.0-6.0	A,S*	5*	B	0.58-0.71	0.42-0.67	A	L,A,B	S	2-4	S,L	B,M
Proceromyia	3.0-5.5	S	5,8-12	B¹,D¹	0.78-0.84	0.34-0.43	A	A	S	1.5-3	S,L	B
Entomophaga	3.0-5.0	A,S	5*	B	0.63-0.77	0.58-0.66	A	B,S	L	3-4	S	B
Ceromya s.s.	3.0-6.0	A*,S	5*	B	0.68-0.86	0.38-0.80	A*,B¹	L→S	S	1.5-10	T→L	B→S
Ceromya silacea group	3.0-5.5	A	5*	B	0.77-0.86	0.47-0.56	A	L→T	S	1.5-5	S,L	M,P
Actia	2.5-6.0	A*,S	5*	B	0.65-0.89	0.43-0.75	A*,B¹	L,A,B	S	1.5-5	T→L	B→S
Peribaea	2.5-5.0	A*,S	5*	B	0.73-0.86	0.39-0.75	A*,B¹,T²,P³	L,A,B	S	1.5-12	T→L*	B→S,M*
Siphona sensu lato												
S. (Actinocrocuta)	3.5-4.5	A	5*	B	0.76-0.81	0.41-0.52	A	A	S	1.5	L	P,S
S. (Aphantorhapha)	2.0-3.5	A,S	5*	B	0.71-0.83	0.43-0.54	A	L,A,B	S	2-4	T→L	M→S
S. (Aphantorhaphopsis)	3.0-5.0	A,S	5*	B	0.69-0.89	0.38-0.63	A	L→S	S	1.5-4	T→L*	B→S
S. (Baeomyia)	2.0-3.0	S	5*	B	0.65-0.83	0.39-0.56	A	A,B,S	L	2-5	V	B
S. (Ceranthia)	3.0-5.5	A,S*	5*	B	0.69-0.88	0.42-0.66	A	B,S	S	2-8	S	B,M
S. (Pseudosiphona)	2.0-5.0	A,S	5*	B	0.73-0.86	0.38-0.48	A	L→S	S,E¹	1.5-2	T→L	M→L
S. (Siphona)	2.5-6.5	A,S	5*	B	0.62-0.91	0.40-0.75	A	L→T	S*,E,L	2-10	T→L*	B,M
S. (Siphonopsis)	2.5-4.5	A,S	5*	B	0.73-0.84	0.37-0.65	A	A→T	S,E²	1.5-6	T→L	B→S
S. (Uruactia)	4.0-5.0	A	5*	B	0.84	0.48-0.50	A	A,B	S	2	L	M
Siphona s.l., sp. grp. 1	3.0-5.0	A,S¹	5*	B	0.67-0.83	0.45-0.67	A	L→T	S,E²	2-8	T→L	M,P
Siphona s.l., sp. grp. 2	2.5-4.5	A*,S	5*	B	0.78-0.86	0.42-0.54	A	L→S	S	1.5-3	S,L*	M→S
Siphona s.l., sp. grp. 3	3.0-4.0	A	5*	B	0.75-0.82	0.43-0.71	A	L→T	S	2-5	T→L	M,P
Siphona s.l., unplaced	3.0-5.0	A*,S	5*	B	0.69-0.91	0.39-0.55	A	L→T	S	1.5-4	T→L	M→S

Lettered states are coded as follows (also see text). Character 2: A, anterior seta longer than posterior one; S, anterior and posterior setae subequal in length. Character 4: B, bare; D, densely haired. Character 7: A, average; B, bilobed; T, trilobed; P, pectinate. Character 8: L, linear; A, average; B, broad; S, subquadrangular; T, large and triangular. Character 9: S, short; E, slightly elongate; L, longer than wide. Character 11: V, very short; T, short and thickened to near tip; S rather short and usually evenly tapered to tip; L, long and evenly tapered to fine tip. Character 12: B, almost bare; M, micropubescent; P, pubescent; S, short plumose; L, medium plumose.

Table 1 (cont.). Distribution of character states in the Siphonini.

Character / Taxon	13 Clypeus shape	14 Palpus shape	15 Prementum length	16 Labella shape	17 Prosternal setation	18 Proepimeral seta	19 Anepisternal setation	20 Katepisternum mid coxa	21 Katepisternum setae	22 Postsutural dorsocentrals	23 ad seta fore tibia	24 ad seta mid tibia
Goniocera	U	S	S	P	B,S	A	$0^2,1^1$	B	S	$3,4^1$	S^1,E^2	2-7
Proceromyia	U^1	S	S	P	B	A	$1^1,3^1$	B	S	3	E	1
Entomophaga	U	L	S	P	S	A	1	B^1,S^1	S	$3^1,4^1$	E	1
Ceromya s.s.	N→U*	S*,L	S	P,S¹	B^1,S*	A	$0^1,1$	B	S,E²	3,4	S,E²	$0^1,1$
Ceromya silacea group	U	S	S	P	S	A	1	B	S,E¹	3,4	S	1
Actia	N→U	S*,L	S*→E	P*→L	B¹,S	A	$1^2,2$	B,S*	S	3,4*	S*,E	$0^1,1$
Peribaea	S,U*	S	S*,M	P	S	P	1*,2	B	S→L	4	S	1
Siphona sensu lato												
S. (Actinocrocuta)	N,S	S	S,M	P→M	S	A	1	B	L	3	S	1
S. (Aphantorhapha)	N,S	S	S,M	P,S¹	S	A	1	B	E,L	3	S	1
S. (Aphantorhaphopsis)	N→U	S*,L,C²	S*→E	P*→L	B¹,S	A	1*,2	B	E,L	3,4	S,E¹	$1,2^2$
S. (Baeomyia)	U	C	S	P	B,S	A	1	B	S,E	3	S	0
S. (Ceranthia)	N→U	S	S	P	S	A	1*,2	B	L	3,4	S	1
S. (Pseudosiphona)	N,S	S	S,M*,E	S→L,M*	S	A	1,2	B	E,L	3	S	1
S. (Siphona)	N	L	E	L	B,S*	A	1*,2	B	E,L*	3,4	S	1
S. (Siphonopsis)	N	S	S,M	E	S	A	1	B	L	3	S	1
S. (Uruactia)	N¹,S¹	S	M	P	S	A	1,2	B	L	$3^1,4^1$	S	1
Siphona s.l., sp. grp. 1	N	S*,L	M*→E	P→E*	S	A	1,2¹	B	L	$3,4^2$	S,E¹	1
Siphona s.l., sp. grp. 2	N*,S	S	S,M	P,E¹	S	A	1	B	L	3	S	1
Siphona s.l., sp. grp. 3	N	S	S,M	P,S¹	S	A	1,2¹	B	L	3	S	1
Siphona s.l., unplaced	N*→U	S*,L	S*→E	P*,S,L²	B¹,S	A	1*,2	B	S,E,L*	3*,4	S	1

Lettered states are coded as follows (also see text). Character 13: N, narrow and partially enclosed in membrane; S, slightly broadened; B, distinctly broadened; U, U-shaped. Character 14: S, short and clavate; L, long and clavate; C, cylindrical. Character 15: S, short; M, medium; E, elongate. Character 16: P, padlike; S, slightly lengthened; M, moderately lengthened; E, elongate; L, as long or longer than prementum. Character 17: S, setulose; B, bare. Character 18: A, absent or hair-like; P, strong and directed downward. Character 20: B, bare; S, row of hairs present. Character 21: S, lower seta shorter than upper anterior seta; E, lower and upper anterior setae subequal in length; L, lower seta longer than upper anterior seta. Character 23: S, shorter than preapical *d* seta; E, subequal or longer than preapical *d* seta.

Table 1 (cont.). Distribution of character states in the Siphonini.

Character	25	26	27	28	29	30	31	32	33	34			
	Tarsomere 5	Claw	Vein R_1		R_{4+5}	CuA_1	Other	Loss of	Anal	Position of crossvein dm-cu			
Taxon	modification	length	dorsally	ventrally	dorsally	dorsally	veins	vein M	vein	spp.	range	mean	SD
Goniocera	A	S,M	B	B	E	B	A	C	N	4	0.26-0.47	0.34	0.08
Proceromyia	A	L	B	B	P	B	A	C	N	2	0.24-0.32	0.27	0.03
Entomophaga	A	S¹,M¹	B	B	P	B	A	C	N	2	0.25-0.43	0.33	0.07
Ceromya s.s.	A*,F,L¹	S*,M	B,D,E	B,D	P¹,E*	B,S,P*	A,B	C	N	39	0.24-0.67	0.40	0.10
Ceromya silacea group	A	S	B,D,E	B,D	E	B,S	A	C	N	5	0.29-0.47	0.36	0.08
Actia	A*,F,L¹	S	B,D,E	B,D	P,E	B,S	A,C,F	N,C*	N,E¹	56	0.25-1.6	0.56	0.27
Peribaea	A,F¹	S,M*	B,D,E	B,D	E	B*,S	A,M	C	E	31	0.63-1.3	0.84	0.18
Siphona sensu lato													
S. (Actinocrocuta)	A	S	D,E	B	E	B,S	A,S	C	E	2	0.35-0.49	0.42	0.06
S. (Aphantorhapha)	A	S	B,E	B,D	P,E	B	A	C	E	6	0.44-0.85	0.64	0.13
S. (Aphantorhaphopsis)	A	S	B,D	B*,D	P,E¹	B	A	C	E	29	0.26-1.4	0.47	0.23
S. (Baeomyia)	A	S	B,D	B	P	B	A	C	E	5	0.64-1.0	0.85	0.09
S. (Ceranthia)	A	S	B*,D	B,D¹	P,E¹	B	A	C	E	19	0.30-0.51	0.42	0.07
S. (Pseudosiphona)	A	S	B,D,E	B	P,E	B	A	C	E	20	0.36-0.74	0.60	0.10
S. (Siphona)	A*,F	S→L	B*,D,E	B*,D	P*,E	B*,S	A	C	E	71	0.26-0.67	0.41	0.07
S. (Siphonopsis)	A	S	B,D	B	P	B	A	C	E	16	0.29-0.55	0.43	0.07
S. (Uruactia)	A	S	D	B	P¹,E¹	B	A	C	E	2	0.26-0.46	0.36	—
Siphona s.l., sp. grp. 1	A	S,M¹	B,D	B	P,E¹	B,S	A	C	E	9	0.21-0.66	0.35	0.14
Siphona s.l., sp. grp. 2	A	S	B¹,D,E	B,D¹	P²,E	B,S	A	C	E	10	0.26-0.67	0.51	0.11
Siphona s.l., sp. grp. 3	A	S	B,E¹	B,D¹	P,E	B,S¹	A	C	E	5	0.37-0.68	0.47	0.09
Siphona s.l., unplaced	A	S	B,D,E¹	B,D¹	P,E	B	A	C	E	17	0.22-0.86	0.45	0.15

Lettered states are coded as follows (also see text). Character 25: B, bare; D, setulose distally; E, setulose along length. Character 26: S, short; M, medium; L, large. Character 27: B, bare; D, setulose distally; E, setulose distally. Character 28: B, bare; D, setulose distally. Character 29: P, setulose between base and r-m; E, setulose from base to beyond r-m. Character 30: B, bare; S, setulose; P, additionally setulose proximal to bm-cu. Character 31: A, average; B, veins Sc and R_{4+5} setulose ventrally; C, R_{2+3}, R_{4+5} and M setulose dorsally and ventrally; F, M setulose ventrally; M, R_{2+3} setulose dorsally and ventrally; S, Sc setulose ventrally. Character 32: C, veins complete; N, vein M fades out apically. Character 33: N, fades out before wing margin; E, extended to wing margin.

Table 1 (cont.). Distribution of character states in the Siphonini.

Character	35	36	37	38	39	40	41	42	43	44	45	46
	Abdominal T_{1+2}		T_3,T_5		Male sternum 5			Size of	Ejaculatory	Male pregonite		
Taxon	m. marg.	l. marg.	setation	processes	ap. lobe	med. lobe	Setulation	male T_6	apodeme	shape	modification	seta
Gonlocera	A→S	A→S	A,D	U	A	F	M	D	S,W	L,T¹	A,M¹	A
Proceromyia	A	S	A,D	O	A	R	M	D	W-1.5	A	L	A
Entomophaga	A	S	A,D	U¹,T¹	A	R	M	D	W-2.0	A	A¹,L¹	A
Ceromya s.s.	A	A→S	A*,D,L	O,U,T	A*,S,C¹	R,E,I,F,A	S,M	S→D	0.5-1.5	M*,O,P¹	M*,E,R	A
Ceromya silacea group	A	A→S	A,D	O,T	A	R,I¹	S*→D	S	0.5-S	A¹,S	A	A
Actia	A	A*→S	A*,D	A*,V,O	A	U*,R,E	M	L→D	0.5-2.0,S*	J	S	A
Peribaea	A	A*→S	A*,D¹,L	V,O,T	A	R*,E,I	M	S→D	S→W*	C	A	A
Siphona sensu lato												
S. (*Actinocrocuta*)	A	A,W	A	U	A→C	R	M	?A	S-2.0	A	T	A,T
S. (*Aphantorhapha*)	A	A,W	A	O,U	A,C	R,T	M	A→D	S-1.5	A	A	A→M
S. (*Aphantorhaphopsis*)	A	A→S	A*,D	V¹,O,U*	A*→C	R,T	M	S→D	0.5-1.5	A*,F¹	A	A→M,L¹
S. (*Baeomyia*)	A	A	A	U	A	R	S,M	D	S-1.5	A	A	T
S. (*Ceranthia*)	A	S	A*,L	U	A→C*	R	S,M	L,D	S-1.5	A	A	A¹,L
S. (*Pseudosiphona*)	A	A*,W	A	V¹,U	A*→C	R,T,A	M	A→L	S	J,W*	T	T,F*
S. (*Siphona*)	A*→S	A→S*	A*,L	O,U*	A,C¹	R	S,M*	A,D	S-2.0	A	A	A
S. (*Siphonopsis*)	A	A,W	A	U	C	R,T,A	M	L→D	S-2.0	A*	A	A→M
S. (*Uruactia*)	A	A¹,S¹	A	U	A	I	M	A	S	A	A	A
Siphona s.l., sp. grp. 1	A	A→S	A	U	A*,C	R,E,T,I,A¹	S¹,M	L→D*	N-3.0¹	A	A,T*	A*→M
Siphona s.l., sp. grp. 2	A	A→S	A*,D	U	A*,C	R,E,T,I,A	M	S→D	0.5-S	A	A,T,L	A→M
Siphona s.l., sp. grp. 3	A	A	A	U	A	R,E,T,A¹	S¹,M	L→D*	0.5-1.5	A	L	A/T¹,T,M
Siphona s.l., unplaced	A	A*→S	A,D¹	V¹,O,U*	A*,C	R,E,T,I,A¹	S,M*	S→D	0.5-1.5	A	A*,T	A→M

Lettered states are coded as follows (also see text). **Character 35**: A, absent; W, weak; S, strong. **Character 36**: A, absent; W, weak; S, strong. **Character 37**: A, average; D, lateral discal setae present; L, extra pair of lateral marginal setae. **Character 38**: A, V-shaped, *Actia*-type; V, V-shaped but with median lobes differentiated; U, U-shaped; O, obtusely angled; T, transverse posteriorly. **Character 39**: A, average, directed posteriorly; S, slightly curved inward; C, distinctly curved inward. **Character 40**: U, undifferentiated; R, rounded; T, truncate; E, elongate; F, broad flattened plate; I, intermediate between states T and F; A, accessory lobe present. **Character 41**: S, sparsely setulose; M, moderately setulose; D, densely setulose. **Character 42**: A, unsclerotized; S, small lateral sclerites; L, large lateral sclerites; D, dorsally continuous sclerite. **Character 43**: N, narrower than hypandrial apodeme; S, subequal in width; W, slightly wider than hypandrial apodeme. **Character 44**: A, average, smoothly curved; C, C-shaped; F, fused with hypandrial apodeme; J, J-shaped; L, linear and slightly curved; M, membranous portion enlarged; O, ring-shaped; P, curved posteriorly; S, sickle-like; T, apically truncate; W, broadened with short pointed apex. **Character 45**: A, spinules absent; L, longitudinal ridge of spines; M, membranous portion enlarged and usually spinulose; E, similar to M but sclerotized portion spined; R, ring-shaped with spinules; S, sclerotized portion spined; T, sclerotized portion with tiny spinules. **Character 46**: A, absent; T, tiny; M, short to medium-sized; L, long and thick; F, two to few short setae.

Table 1 (cont.). Distribution of character states in the Siphonini.

Character Taxon	47 Epiphallus size	48 posterior	49 Male distiphallus posterolateral	50 lateral	51 Postgonite shape	52 Male surstylus basally	53 shape	54 Cerci shape	55 Female ovipositor	56 Female sternum 6
Goniocera	N	I	S	A	W	F	L	I	M	A
Proceromyia	A¹,S¹	I	A	P	W	M	A	A¹,S¹	S¹	A¹
Entomophaga	S¹,N¹	I	A	P	W	M	A¹,C¹	S	S¹	A¹
Ceromya s.s.	A,N,P	E²,I	A→E	A*,P	W	M,F*	A,B,S,C,L	A,S,I	S→E	A
Ceromya silacea group	A,N¹	I	A→E	A,P¹	W	M,F	A,C,L	A,S,I	S¹	A¹
Actia	A	I	A	A*,P	W	M	A,B,S,L	A,S,R,I	S	A
Peribaea	A,N,P	E	A	A,P²	W	M*,F	A,B,C,L	A,S,L,R*	S*→E,V¹	A*→E,W,S
Siphona sensu lato										
S. (Actinocrocuta)	A	I	A	A,P	W,S¹	M	A,S	L	M¹	W¹
S. (Aphantorhapha)	A	I	A	A,P	W	M	A,S,L	A,R²	S¹	A¹
S. (Aphantorhaphopsis)	A,N,S¹,P¹	I	A→E	A*,P	W,R²	M,F¹	A,B,S,C,L	A*,S,I	S	A
S. (Baeomyia)	A	I	A	A	W,S	M	A,C	A,S,I	S	A
S. (Ceranthia)	A	I	M,E*	A,P	W	M	A	A	S→E	A,W,M²
S. (Pseudosiphona)	A	I	A	A,P*	W	M	A,B,C,L	S→E,B,I*	S*→M	A*,W¹,S¹
S. (Siphona)	A	I	A,M¹	A*,P	W	M	A*,L	A	S	A
S. (Siphonopsis)	A	I	A	A	W,S,R¹	M	A,L¹	A*,S,B	S	A
S. (Uruactia)	A	I	A¹,M¹	P	W	M	L	I	—	—
Siphona s.l., sp. grp. 1	A	I	A	A	W→R*	M	A,B,S,C,L	A,B¹	S	A
Siphona s.l., sp. grp. 2	A	E¹,I	A→E	A	W,S¹,R²	M	A,C,L	A,R,L	S	A
Siphona s.l., sp. grp. 3	A	I	A	A,P¹	W,S¹,R¹	M	A	A	S¹	A¹
Siphona s.l., unplaced	A	I	A→E	A*,P	W*,R²	M	A*,S,C,L	A,S¹,B¹,E¹,L²	S	A,S¹

Lettered states are coded as follows (also see text). Character 47: A, absent; S, small; N, narrow; P, average-sized. Character 48: E, entirely sclerotized; I, incised. Character 49: A, not incised posterolaterally; S, not extended beyond apex of lateral margin; M, moderate extension; E, extended well beyond rest of distiphallus. Character 50: A, small spinules only; P, anterior and/or apical margin spined. Character 51: W, large; S, short; R, reduced. Character 52: M, membranous; F, narrowly connected with epandrium. Character 53: A, average; S, short; B, broad; C, curved posteriorly; L, elongate. Character 54: A, average; S, short; B, broadened; E, elongate; L, linear; R, same as L but short; I, sharply inflexed at midlength. Character 55: S, short; M, moderately extensible; E, elongate; V, very elongate. Character 56: A, average; W, slightly keeled posteromedially; S, sharply keeled posteromedially; M, moderately elongate; E, elongate.

Table 1 (cont.). Distribution of character states in the Siphonini.

Character	57	58	59	60	61	62	63	64	65	66	67
Taxon	Female tergum 6	Female sternum apodeme	Female sternum 7 shape	Female tergum 7	Segment 7 spiracle	Female sternum 8	Female tergum 10	1st instar labrum	Dorsal cornu	Posteroventral margin abd. seg. 6	Posteroventral margin abd. seg. 7
Goniocera	L	A	A[1],W[1]	L	I	R	P	B[1]	P[1]	B[1]	R[1]
Proceromyia	N[1]	W[1]	A[1]	L[1]	A[1]	A[1]	M[1]	—	—	—	—
Entomophaga	N[1]	W[1]	W[1]	L[1]	A[1]	L[1]	A/R[1]	I[1]	P[1]	B[1]	R[1]
Ceromya s.s.	S,L,N	A*→W	A*,W,S[1]	A→L	P,I*,A	A	A,M,P	I[1],B	P	B,10[1]	R*,S
Ceromya silacea group	L[1]	W[1]	A[1]	L[1]	P[1]	A[1]	P[1]	N[1]	P[1]	B[1]	R[1]
Actia	A,S,L,N	A,S[1]	A	A,S	I	A	M	B	A,?P[1]	B	R*,S
Peribaea	L,D	A	A*→L,W,S	S,L*,F	P	L→A*,B	A,R,M	N,I[1]	P	B	R
Siphona sensu lato											
S. (Actinocrocuta)	A[1]	W[1]	W[1]	A[1]	?	W[1]	P[1]	B[1]	P[1]	4[1]	S[1]
S. (Aphantorhapha)	A/M[1]	W[1]	A[1]	A/S[1]	I[1]	A[1]	P[1]	B[1]	P[1]	4[1]	S[1]
S. (Aphantorhaphopsis)	A,?	W	A	A,S[1]	I	A*,W	A[1],R,M,P	B	P	B[1],2[1],4-8	S
S. (Baeomyia)	A	W	A	A	I	A	A	B	P	6-8	S
S. (Ceranthia)	A	W	W,S,L	A	P	A	P	B	P	6-8	S
S. (Pseudosiphona)	A	W,S[1]	A→L,W,S	A,S[1],L[1]	I,A[1]	A,B[1],S[1]	M,P	N*,I	P	2[1],4[1],4-8	R,S[1]
S. (Siphona)	A	W	A	A	P	A	A,R	B	P	4	S
S. (Siphonopsis)	A,S,M	W*,S	A,L[1]	A,S[1]	I	A	M*,P	B	P	4	S
S. (Uruactia)	—	—	—	—	—	—	—	—	—	—	—
Siphona s.l., sp. grp. 1	A	W	A	A	I	A,W[1]	R,M,P	B	P	2[1],5[1]	S
Siphona s.l., sp. grp. 2	D	W	A	L	P	W	M,P	B[1]	P[1]	4[1]	S[1]
Siphona s.l., sp. grp. 3	D[1]	W[1]	A[1]	A[1]	I[1]	A[1]	P[1]	B[1]	P[1]	4[1]	S[1]
Siphona s.l., unplaced	A,S,D[1]	W,S[1]	A,S[1]	A→L,F[1]	I,P[2]	A,W[1],S[1]	R,M,P	B	P	4[1],6[1],10[1]	S

Lettered states are coded as follows (also see text). Character 57: A, absent; S, very small lateral sclerites; L, moderate-sized lateral sclerites; M, dorsomedian sclerite; D, single sclerite extended dorsally and laterally; N, as in D but narrowly discontinuous dorsally. Character 58: A, absent; S, short; W, long. Character 59: A, average; W, slightly keeled posteromedially; S, sharply keeled posteromedially; E, elongate; L, elongate and keeled posteromedially. Character 60: A, absent; S, very small lateral sclerites; L, moderate-sized lateral sclerites; F, lateral sclerites fused with S. Character 61: P, posterior; I, intermediate; A, anterior. Character 62: A, average; L, lacking; R, reduced; W, wider than average; B, bare; S, thick setae posteriorly. Character 63: A, absent; R, reduced; M, median sclerite; P, paired sclerites. Character 64: N, narrow; hook-like; B, broadened, hatchet-like; I, intermediate, slightly broadened. Character 65: P, present; A, absent. Character 66: B, bare or small spinules. Character 67: R, two or more rows of spinules; S, single dominant row of spinules.

CLASSIFICATION OF THE SIPHONINI

List of major references to the Siphonini

Thryptoceratae Robineau-Desvoidy 1830: 82-102 (unavailable name).

Siphonae Rondani 1845: 31 (original description).

Siphonina Rondani 1856: 59 (*Siphona*; other siphonine genera in Tachinina).

Siphoninae Rondani 1859: 9-11 (Italian species of *Siphona*; other siphonines in Tachininae).

— [Muscidae], Schiner 1862: 517-522 (early classification; species of Austria).

Céromydes and Thryptocérides, Robineau-Desvoidy 1863: 665-728 (early classification).

Thryptoceratidae, Brauer and Bergenstamm 1889: 101-106 (early classification).

Section *Thryptocera*, Brauer and Bergenstamm 1893: 148-152 (early classification).

—, Bezzi and Stein 1907: 381-392 (early Palearctic catalogue).

Section *Thryptocera*, Villeneuve 1924: 34 (Palearctic reclassification).

Group *Thryptocera*, Stein 1924: 123-148 (reclassification and revision of mid-European species).

— [Eutachininae, Group 3], Lundbeck 1927: 448-476 (species of Denmark).

— [Tachininae], Wainwright 1928: 203-209 (species of Britain).

Actiini, Malloch 1930a: 303-310 (species of Australia, all as *Actia*).

Actiini, Malloch 1930b: 120-148 (species of Malaysia, all as *Actia*).

Actiini and Siphonini, Townsend 1936: 129-152 (tribal descriptions and generic keys; very broad tribal limits).

Crocutini, Mesnil 1939: 35-36 (reclassification).

Actiini and Siphonini, Townsend 1940: 187-299 (generic descriptions following 1936 classification).

Siphonini, Emden [van Emden] 1954: 62-68 (species of Britain).

Siphoninae, Mesnil 1954, 41 pp. (reclassification and species of "Congo Belge").

Siphona group, Herting 1957: 454, 458 (female genitalia).

Siphonini, Herting 1960: 58-63 (biology of Palearctic species).

Siphonina, Mesnil 1962-1965: 795-879 (reclassification and revision of Palearctic species).

Siphonina, Sabrosky and Arnaud 1965: 1061-1064 (list of New World species north of Mexico).

Siphonini, Mesnil and Pschorn-Walcher 1968: 163-164 (list of species of Japan).

Siphonini, Guimarães 1971: 164-171 (list of New World species south of United States; broad tribal concept).

Siphonini, Crosskey 1973: 80-81, 136-138, 176 (species of Australia).

Siphonini, Mesnil 1975: 1399-1400 (changes to 1962-1965 Palearctic revision).

Siphonini, Crosskey 1976a: 112-113, 211-214, 291 (species of Oriental region).

Siphonini, Crosskey 1976b: 99-100 (list of British species).

Siphonini, Crosskey 1980: 852-855 (list of Afrotropical species).

Siphonini, Dear and Crosskey 1982: 134-139 (species of the Philippines).

Siphonini, Andersen 1983: 1-15 (revision of Old World genera).

Siphonini, Crosskey 1984: 261-262 (key to Afrotropical genera).

Siphonini, Herting 1984: 120-126 (list of Palearctic species).

Siphonini, Tschorsnig 1985: 88-89 (male genitalia).

Siphonini, Rognes 1986: 72-73 (list of Norwegian species).

Diagnosis of adults of Siphonini Rondani

The most convincing synapotypy, and hence best diagnostic feature, of the Siphonini is the presence of only two (rather than three) spermathecae in the female reproductive system. This state seems to be universal among siphonines, and is known to be shared with only one other (unrelated) tachinid genus, *Phaenopsis* Townsend (Andersen 1983).

The following combination of character states separates adults of this tribe from other tachinids: Generally 3.0-5.0mm in length, but varied from 2.0-6.5mm. Head (Figs. 1-20) with little sexual dimorphism. Two proclinate orbital setae in both sexes. Eye bare or almost so and three to five frontal setae except in *Proceromyia*

pubioculata (eye densely haired and 8-12 frontals; Fig. 3). Aristomere 2 longer than wide, elongate in most species. Proboscis varied from short to long, labella padlike to more than 2X head height.

Thoracic dorsum illustrated in O'Hara (1983a, fig. 2). Prosternum with one to several pair of setulae in most species, bare in a few (intraspecifically varied in a few species). Katepisternum with three setae arranged in triangle (Figs. 31-32), lower seta varied from hairlike to slightly longer than upper anterior seta. Row of katepisternal hairs anterior to mid coxa present (Fig. 33) or absent (Fig. 34). Three or four postsutural dorsocentral setae. Scutellum with strong basal, lateral and subapical setae, subapicals longest and convergent to crossed, apicals short in most species. One *ad* seta on mid tibia (Fig. 37) in most species, seta absent from a few species (Fig. 38) and row of setae present in *Goniocera* species. Wing relatively short and broad (Figs. 21-22), vein R_1 partially incised at midpoint, vein R_{4+5} setulose dorsally from bifurcation of R_{2+3} and R_{4+5} to crossvein *r-m* or beyond, vein *m* smoothly curved in apical sector and ending in wing margin near wing tip (ending close to end of R_{4+5}), anal vein extended to or not extended to wing margin.

Abdomen (O'Hara 1983a, figs. 7-8) ovoid to elongate, with T_{1+2} excavate on basal half. Median discal setae absent from T_{1+2} to T_4. T_{1+2} with 0-1 pair of lateral marginal setae in most species, additional pair present in a few species, pair of median marginal setae present in a few species of *Goniocera* and *Siphona (Siphona)*. T_3 to T_4 with strong pair each of lateral and median marginal setae, additional marginals present in a few species. T_5 with row of marginal setae and in a few species with row of weak discal setae.

Male genitalia (O'Hara 1983a, fig. 9) with tergum 6 unsclerotized to moderately broad and sclerotized. Terga 7+8 well developed. Epandrium saddle-shaped. Pregonite (Figs. 39-42, 71-106) well developed, with membrane anteriorly between apex and basal articulation with hypandrium (possibly synapotypic of the Siphonini, as suggested by Tschorsnig 1985 and discussed in Evolution chapter). Ejaculatory apodeme well developed. Aedeagus with or without an epiphallus. Distiphallus (Figs. 107-136) narrowly connected to basiphallus, in most species approximately cylindrical in shape and well sclerotized laterally. Postgonite well developed to markedly reduced. Surstylus (Figs. 137-141) linear, relatively unmodified, and basally free or connected with epandrium by a narrow strap-like connection. Cerci (Figs. 142-144) medially incised basally, fused apically.

Female reproductive system with two spermathecae (synapotypic of the Siphonini). Female genitalia (Figs. 43-46, 145-156) unmodified to long and extensible (telescopic), without piercing ability. Tergum 6 absent to dorsally continuous. Tergum 7 absent to present as two moderate-sized lateral sclerites. Spiracle of segment 6 associated with ventrolateral margin of tergum 6, spiracle of segment 7 varied in position from segment 7 to segment 6. Tergum 8 represented by two lateral sclerites, sternum 8 relatively narrow in most species, absent from a few. Segment 9 without external sclerites (O'Hara 1983c: 380). Tergum 10 unsclerotized

or represented by small median sclerite or two small sclerites. Sternum 10 and paired cerci unmodified.

Review of major keys to genera and subgenera of the Siphonini

Keys to genera and subgenera of the Siphonini are available for each of the biogeographic regions of the world except the Neotropics. Each key reflects a classification different from the one adopted here, so each also differs from the keys presented in this work: *i.e.* key to the genera of the Siphonini, keys to the species of *Proceromyia* and *Entomophaga*, and key to the subgenera of *Siphona s.l.* To avoid confusion between those keys and mine, the major differences are summarized here. Specific information about differences in the placement of species can be obtained by comparing the species lists accompanying most of the works cited below with the descriptions and species lists contained herein. Differences in phylogenetic interpretation are not discussed in this section, but rather in the Phylogenetics section of each supraspecific taxon described. Recent keys to species are cited in the Geographic Distribution section of each supraspecific taxon.

The keys considered here are those published in major works since Mesnil's revision of the Palearctic Siphonini in "Die Fliegen der palaearktischen Region" (1962-1965). The most geographically comprehensive is Andersen's (1983) generic revision of the Old World Siphonini. This work is broad in scope and contains important new findings about the Siphonini. Andersen's key (pp. 13-14) is easy to use and his classification is similar to the one presented herein. His key differs from mine in the following respects: the two species of *Entomophaga* are split between *Actia* and *Ceromya*, *Proceromyia macronychia* is included in *Ceromya*, *Proceromyia pubioculata* (type species of *Nipponoceromyia*) was not examined and hence excluded, *Actia* species with atypical features key to *Ceromya* or *Asiphona*, taxa here considered subgenera of *Siphona s.l.* are considered genera, *Siphona (Aphantorhaphopsis)* is called *Asiphona*, a few species of *S. (Aphantorhaphopsis)* key to *Ceranthia*, and *S. (Aphantorhaphopsis)* and *S. (Siphona)* [his *Asiphona* and *Siphona*, respectively] not adequately differentiated. Most of these differences stem from the relatively few species examined by Andersen during his study. Most of the species which key differently have limited known ranges (mostly non-Palearctic) and/or are rarely collected, so despite the differences in our keys probably 90% of Old World siphonine species will key to the same taxon. Because my keys attempt to provide for accurate generic placement of all species examined (see Materials and Methods), they are necessarily longer and more complex than Andersen's.

Other keys to Old World siphonine genera and subgenera are regional in coverage. The most comprehensive is Mesnil's Palearctic revision cited above (1962-1965), in which all the then known species of Palearctic Siphonini are keyed and described. Mesnil's revision restructured the concept of the Siphonini into its modern form and still provides the only means for identification of most species of Palearctic Siphonini. With respect to the Palearctic fauna, Mesnil's keys to the

Siphonini (1962: 797) and subgenera of *Ceromya* (1963a: 829) differ from mine as follows: *Peribaea* called *Strobliomyia*, *Siphona (Aphantorhaphopsis)* called *Siphona (Asiphona)*, *Ceranthia* accorded generic rank, *Proceromyia* as *Ceromya (Proceromyia)*, *Entomophaga exoleta* in *Actia*, *Ceromya monstrosicornis* as type species of *Ceromya (Stenoparia)* and *Entomophaga nigrohalterata* as *C. (Stenoparia) nigrohalterata*. *Nipponoceromyia* (here synonymized with *Proceromyia*) was described after Mesnil's revision. Atypical species of *Actia* and *S. (Aphantorhaphopsis)* are non-Palearctic in distribution.

The remaining Old World regions have received recent treatment by Crosskey. These include a conspectus of Australian Tachinidae (1973), conspectus of Oriental Tachinidae (1976), review of the Tachinidae of the Philippines (Dear and Crosskey 1982), catalogue of Afrotropical Tachinidae (1980, including Madagascar) and key to genera of Afrotropical Tachinidae (1984, excluding Madagascar). Excluded from these works is a treatment of the Tachinidae of the Australian region outside Australia. These works follow the same classification of the Siphonini, so their keys are here compared as one with the keys herein: atypical *Actia* species key to *Ceromya*, *Siphona s.s.* not then recorded from Australia, *S. (Aphantorhaphopsis)* generally not recognized so most of its species are placed in *Ceromya* and a few (those with elongate labella) in *Siphona s.s.*, and ranking of subgenera of *Siphona s.l.* as genera. These differences in classification are mitigated by Crosskey's comprehensive species lists for each region, without which the initial stages of almost any revision of a non-Palearctic tachinid group would be an arduous task.

Wood's (1987) recent key to tachinid genera of the Nearctic region provides a valuable and much needed guide to the identification of Nearctic Tachinidae. Wood separates tachinid genera in the first couplet of his key according to presence or absence of setulae on the prosternum. *Goniocera io* (the only New World species of the genus) is varied for this character, though it keys as having a bare prosternum. Other siphonines key as having a setulose prosternum, though a few of these species are also intraspecifically varied for this character (especially species of *Siphona (Baeomyia)*). Wood's *Siphona* and *Baeomyia* are equivalent to my *Siphona (Siphona)* and *S. (Baeomyia)*, and his *Ceranthia* includes all Nearctic *Siphona s.l.* species exclusive of the last two subgenera.

Key to adults of the genera of the Siphonini

1   Lower proepimeral seta strong and directed downward (Fig. 27)
           (Old World) ....*Peribaea* R.-D., p. 77
1'   Lower proepimeral seta absent or hair-like (Fig. 28) 2
2   (1') Anal vein not extended to wing margin (Fig. 21); lower
           katepisternal seta shorter than upper anterior one (Fig. 31) 3
2'   Anal vein extended to wing margin at least as fold (Fig. 22);
           lower katepisternal seta subequal to or longer than upper

anterior one in most species (Fig. 32).. 10

3   (2)   Mid tibia with row of three or more *ad* setae and setulae (four species; Europe and northeastern North America) ....
....*Goniocera* B. & B., p. 41

3'   Mid tibia with one *ad* seta in most species (Fig. 37), seta reduced or absent in a very few (Fig. 38) 4

4   (3') Aristomere 1 distinctly longer than wide (Figs. 4-5) *and* fore tibia with preapical *ad* seta as long as or longer than *d* seta (two European species) .... *Entomophaga* Lioy, p. 47

4'   Most species with aristomere 1 distinctly shorter than wide and fore tibia with preapical *ad* seta shorter than *d* seta, a few species with one (but not both) of above states 5

5   (4') Katepisternum with row of hairs directly anterior to mid coxa, extended upward almost to lower katepisternal seta (Fig. 33) (cosmopolitan) .... most species of *Actia* R.-D., p. 67

5'   Katepisternum almost bare directly anterior to mid coxa, except for several hairs in posteroventral corner (Fig. 34) 6

6   (5') Male sternum 5 with posterior margin approximately V-shaped (Figs. 58-59); pregonite with outer, sclerotized portion short spinose on apical half or less (Figs. 41-42, 85-86); upper part of anepisternum with two setulae (Fig. 31) (presently known only from Malaysia and eastern Australia)...
....several species of *Actia* R.-D., p. 67

6'   Male sternum 5 with posterior margin U-shaped, obtusely angled or almost transverse (Figs. 48-49, 52-57); pregonite bare or with tiny to distinct, uniformly-sized spinules (Figs. 39-40, 73-74, 77-84) (spinules, if present, restricted to membranous portion of pregonite except in several species with extensively sclerotized, ring-shaped pregonite, Fig. 78); upper part of anepisternum with one setula in most species (Fig. 32) 7

7   (6') Dorsal surface of wing vein R_{4+5} setulose from base to beyond crossvein *r-m* (as in Fig. 21) (cosmopolitan)..................................
.... most species of *Ceromya* R.-D. *sensu lato*...................... 8

7'   Dorsal surface of wing vein R_{4+5} setulose between base and crossvein *r-m* (as in Fig. 22) (Old World) 9

8   (7)   Distiphallus bearing unique, infolded and sclerotized structure formed from posterior surface (Fig. 112); pregonite bare (Fig. 84) (Old World) ..... *Ceromya silacea* (Mg.) species group, p. 63

8'   Distiphallus without infolded and sclerotized structure (Figs. 113-116); pregonite bare in a few species (Fig. 77), with tiny to distinct spinules in most species (Figs. 78-83) (spinules, if present, restricted to membranous portion of pregonite except

in several species with extensively sclerotized, ring-shaped pregonite - Fig. 78); (cosmopolitan)..
....*Ceromya* R.-D. *sensu stricto*, p. 52

9   (7')   Fore tibia with preapical *ad* seta as long as or longer than *d* seta; male genitalia with distinctive sternum 5 (Figs. 48-49), pregonite (Figs. 73-74) and distiphallus (Figs. 108-109)... *Proceromyia* Mesnil, p. 44

9'   Fore tibia with preapical *ad* seta shorter than *d* seta; male genitalia not as above in *C. cephalotes* and *C. natalensis*, not examined in *C. monstrosicornis* (these species discussed in Phylogenetics section of *Ceromya s.s.*) ....
........three known species of *Ceromya* R.-D. *sensu stricto*, p. 52

10 (2')   Katepisternum with row of hairs directly anterior to mid coxa, extended upward halfway to lower katepisternal seta (type specimen of *A. completa* from Malaysia) or almost to lower katepisternal seta (as in Fig. 33; *A. fulvicauda* from Malaysia and *A. chrysocera* from the Seychelles Islands)...........................
.... three known species of *Actia* R.-D., p. 67

10'   Katepisternum almost bare anterior to mid coxa, except for several hairs in posteroventral corner (Fig. 34)...........................
....*Siphona* Meigen *sensu lato*, p. 84
            [Subgenera keyed in section on *Siphona s.l.*]

Notes about classification chapter

Notes about lists of included species.— The present classification of the Siphonini includes 386 named species (excluding *nomina nuda* and misspellings), of which 294 are recognized as taxonomically valid species. Each description of a supraspecific taxon of the Siphonini is followed by a list of included species. Names of species treated as valid are preceded by a letter indicating the region of occurrence of the species, and all named species are followed by full bibliographic and type information (sex, type locality and depository, and whether type examined). Synonyms are listed in chronological order according to date of description. The following letters are used to denote region(s) of occurrence of each species:

A   Afrotropical, *sensu* Crosskey and White (1977).
N   Nearctic, *sensu* Griffiths (1980).
O   Oriental, *sensu* Crosskey (1976a).
P   Palearctic, as delimited by the Afrotropical and Oriental regions.
S   Neotropical, *sensu* Griffiths (1980).
U   Australian.

Lists of included species were originally compiled from regional catalogues by Sabrosky and Arnaud (1965), Guimarães (1971), Crosskey (1973, 1976a, 1980) and Herting (1984). This information was then checked and where necessary augmented, many of the types personally examined, and the species and genera reclassified into the present scheme. Changes to previous classifications are listed in the next section and are indicated in the lists in bold face. In general, I avoided decisions about species synonymies and followed current placements. This is particularly true of the older Palearctic names that have been authoritatively re-evaluated in the works of Herting (1969-1984). For each listed synonym I have included a recent reference to its synonymic status rather than attempt to determine the author who first proposed the synonymy. In a few instances I have recognized new synonymies or have changed the status of subspecies. Each change of this sort is discussed in the taxonomic portion of this revision under the appropriate genus. Not discussed are new combinations, unless the species involved possesses a combination of character states unusual or atypical of the genus into which it is placed.

Type designations of Coquillett and Townsend.— The type concept became increasingly popular among taxonomists in the late 1800's and early 1900's, and it was not unusual for workers of that period to adopt the concept at some point in their careers. Coquillett and Townsend were two such workers, and it is the status of the type series of their earlier species that is of concern here.

It is evident that Coquillett, by the time of his 1897 "Revision of the Tachinidae", was not only choosing type specimens for new species but for his previously described species as well. He assigned type numbers to each of his USNM types, though only published numbers for species he described as new in the "Revision" (Sabrosky, pers. comm.). For previously described species Coquillett generally appended his redescription with the statement "From the type specimen". For the purposes of nomenclatural stability, and because Coquillett's intent is clear, I accept his reference to a type specimen in the redescription of a species described from syntypes as a valid lectotype designation. (This was also the interpretation of Sabrosky and Arnaud 1963.) Similarly, I accept Coquillett's citation of a type number in the description of a new species as sufficient for a holotype designation, provided specimens were labelled appropriately. Under the first situation two siphonines are involved, *S. (Siphonopsis) plusiae* and *Ceromya palloris*, and under the second *S. (Ceranthia) flavipes* and *S. (Pseudosiphona) brevirostris*. In the text that follows I accept Coquillett's lectotype designations of *S. plusiae* and *C. palloris* and his holotype designation of *S. flavipes*. I have had to designate a lectotype for *S. brevirostris* because Coquillett's original holotype designation refers to a pin bearing two specimens, neither of which was specifically chosen as the type.

There is only one siphonine described by Townsend, *Actinocrocuta chaetosa*, for which a holotype was not designated in the original description. However, in his 1940 redescription of the genus (which is herein considered a subgenus of *Siphona*), Townsend cites the "Ht male" of *A. chaetosa*, clearly indicating his choice of the

only male of the type series as the type. I accept this citation as a lectotype designation.

<p style="text-align:center">Genus Goniocera Brauer and Bergenstamm
Figs. 1, 47, 71-72, 107, 137, 145, 158</p>

Goniocera Brauer and Bergenstamm, 1891: 354. Type-species, *G. schistacea* Brauer and Bergenstamm, 1891 (monotypy).

Euthryptocera Townsend, 1916: 624. Type-species, *Tachina latifrons* Meigen, 1824 (original designation) = *Tachina versicolor* Fallén, 1820.

Euchaetactia Villeneuve, 1921: 47 (as subgenus of *Actia* Robineau-Desvoidy). Type-species, *Actia* (*Euchaetactia*) *montium* Villeneuve, 1921 (monotypy).

Cartocometes Aldrich, 1929: 9. Type-species, *C. io* Aldrich, 1929 (original designation). Recent synonymy by Wood (1987: 1258) in key to Nearctic tachinid genera.

Recognition

This genus of four described species belongs to the group of siphonine genera in which the anal vein does not extend to the wing margin (*i.e.* all genera except *Peribaea* and *Siphona s.l.*), and is distinguished from other members of this group by the presence of several *ad* setae on the mid tibia. Other siphonines have one *ad* seta (Fig. 37) or none (Fig. 38), with the known exception of two undescribed African species of *S. (Aphantorhaphopsis)* which have two setae - these two species have the anal vein extended to the wing margin and other *Siphona s.l.* characteristics. The distinctive shape of the distiphallus is probably autapotypic of *Goniocera* (Fig. 107; refer to Description and Phylogenetics sections).

Three of the four *Goniocera* species have a densely setulose parafacial (Fig. 1). The other species, *G. versicolor*, has the lower parafacial bare (*i.e.* the region of the parafacial adjacent to the lower margin of the eye) as in most other siphonines (several siphonines have hairs on lower parafacial, but fewer hairs than in the three *Goniocera* species). Other features shared by species of *Goniocera*, though only collectively unique to the genus, include (*cf.* Table 1): wing vein R_{4+5} setulose from base to beyond crossvein *r-m* and other veins bare, prominent and flattened median lobe on male sternum 5 (Fig. 47; similar appearance in a few *Ceromya* species), surstylus long and basally fused with epandrium (Fig. 137), and reduced female sternum 8 (Fig. 145). The male and female genitalia of *G. montium* and the female genitalia of *G. versicolor* were not examined, so it is unknown if these species share the genitalic features of the other species.

Description

Length: 4.0-6.0mm.

Head (Fig. 1).— Five frontal setae, normal arrangment. Proclinate orbital setae subequal in size in most species. Lower parafacial bare in *G. versicolor*, densely setulose in other species. Eye of male small to medium, 0.58-0.71 head height; eye of female slightly smaller than in male. Flagellomere 1 of male medium-short to medium-long, 0.42-0.67 head height; shape from linear to slightly broadened; not bifid. Flagellomere 1 of female slightly smaller than in male. Aristomere 1 short. Aristomere two 2-4X longer than wide. Aristomere 3 almost bare to micropubescent, rather short (*G. montium*) to long and tapered. Clypeus

U-shaped. Palpus short to medium, clavate. Proboscis with prementum short, labella padlike.

Thorax.— Prosternum bare or setulose. Lower proepimeral seta weak, not directed downward. Katepisternum bare anterior to mid coxa. Lower katepisternal seta shorter than upper anterior seta. Three postsutural dorsocentral setae, except four in *G. montium*. Upper part of anepisternum lacking, or with single, setula. Fore tibia with preapical *ad* seta varied: short in *G. montium*, half to subequal length of *d* seta in *G. schistacea*, and at least length of *d* seta in *G. io* and *G. versicolor*. Mid tibia with row of *ad* setae, two to seven long and one to three shorter in most taxa. Tarsomeres normal in size, claws small to medium. Wing: CuA_1 with distal portion 0.26-0.47 length of proximal portion (*i.e. dm-cu* near wing margin; mean 0.34); anal vein not extended to wing margin. Wing setulae: R_1 bare dorsally and ventrally; R_{4+5} setulose from base to beyond *r-m*; CuA_1 bare.

Abdominal terga 1-5.— Abdomen ovoid in shape. Setae varied in length intraspecifically: some specimens with median and lateral marginal setae on T_{1+2} and lateral discal setae on T_{1+2}-T_5, others without long setae on T_{1+2} and with normal setation on T_3-T_5.

Male genitalia (Figs. 47, 71-72, 107, 137).— S_5 (Fig. 47) little varied, posterior margin approximately U-shaped; processes with apical lobes clearly differentiated, at least as long as wide; median lobe unusually prominent, in form of broad, truncate plate flattened posteromedially; processes moderately setulose. T_6 in form of single, narrow to broad, dorsally continuous sclerite. Ejaculatory apodeme with fan-shaped portion subequal to or slightly wider than hypandrial apodeme. Pregonite in profile either narrow and linear (Fig. 72), or broad and truncate with membranous portion spinulose (*G. io*, Fig. 71). Epiphallus present, narrow (not absent as stated in Andersen 1983 and shown in his fig. 22). Distiphallus (Fig. 107) large, in profile more or less truncate apically and evenly tapered basally, posterolateral margin with short pointed sclerite (not extended beyond apex of distiphallus) separated from broad lateral margin by narrow incision (posterolateral margin curved toward midline and thus pointed sclerite not visible in Fig. 107), anterior margin distinctly developed; apex at least as long as broad in ventral view. Postgonite apically narrow or broad, turned outward. Surstylus long, thin and straight; fused basally with epandrium (Fig. 137). Cerci elongate, sharply inflexed at midlength; thickly covered with long setae on basal half (Fig. 137). Examined male genitalia of: *G. io, G. schistacea* and *G. versicolor* (last species shown in Andersen 1983, fig. 22).

Female genitalia (Fig. 145).— Moderately extensible. S_6 with very long hairs. T_6 distinctly developed, enclosing spiracles of segment 6; discontinuous dorsally. S_7 without anterior apodeme; pointed posteriorly, with (*G. schistacea*) or without (*G. io*) posteromedial keel. T_7 present as two lateral sclerites; spiracles of segment 7 in membrane between segments 6 and 7. S_8 small, haired. T_{10} present as two small sclerites. Examined female genitalia of: *G. io*. Female reproductive system of *G. schistacea* shown in Andersen (1983, fig. 3).

Hosts

Hosts are known for three of the four species, and these are all parasites of *Malacosoma* species (tent caterpillars) (Table 2).

Phylogenetics

The only externally autapotypic feature of *Goniocera* is the row of *ad* setae on the mid tibia, though similarities in the male genitalia, specifically sternum 5 and distiphallus, in three of the four species (male genitalia of *G. montium* not examined) provide additional evidence supporting monophyly of the genus. With respect to male sternum 5, the median lobe is unusually prominent, and flattened on its posteromedial surface (Fig. 47). A trend in several siphonine groups is toward a flattened median lobe (*e.g.* Figs. 54, 68), but only in a few *Ceromya s.s.* species is its shape similar to that in *Goniocera* species. Considering this trend, and the presumably derived phylogenetic position of these *Ceromya s.s.* species within that genus, it is probable that the characteristic shape of sternum 5 among *Goniocera*

species is a synapotypy, and its similar appearance in *Ceromya s.s.* is the result of convergence.

Shape of the distiphallus is similar among examined *Goniocera* species (Fig. 107). In particular the posterolateral margins are curved toward the midline, and incised to form two short sclerotized projections (one per side) - as these projections are only seen in posterior view they are not visible in Fig. 107. The only other siphonines known to share this feature are two species of the *Ceromya palloris* group, *C. flaviseta* and *C. ontario*, which are not otherwise similar to *Goniocera* species. The male genitalia of *G. montium* were not examined, but it is predicted that they have the same states here suggested as synapotypies of the genus.

The pregonite of *G. io* differs from those of *G. schistacea* and *G. versicolor* by the presence of tiny spinules on the membranous portion (Fig. 71). This feature is in most *Ceromya s.s.* species, and is considered synapotypic of that group. The presence of spinules on the pregonite of *G. io* can be interpreted in several ways, as discussed in the Evolution chapter. These different interpretations of the pregonite in *G. io* lead to different phylogenetic senarios regarding *Goniocera* (Figs. 166-169), but none challenges the well established monophyly of the genus.

Adult females of *G. io* and *G. schistacea* have a small sternum 8 (Fig. 145), which is a derived state among siphonines. The size of this sclerite is unknown in *G. montium* and *G. versicolor*, but if also small, then would represent another synapotypy of the genus.

Tent caterpillars (*Malacosoma* species, Lasiocampidae) are the only known hosts of *Goniocera* species (Table 2). Since *G. montium* is the only *Goniocera* species for which a host is unrecorded, and *Malacosoma* species are not known hosts for any other siphonines, I hypothesize that this parasitic specialization is a synapotypy of *Goniocera* species.

Geographic distribution

This genus includes three sympatric species in the Palearctic region, all western in distribution (Mesnil 1963a, Herting 1984): *G. montium* (a rarely collected species only known from France), *G. schistacea* (Denmark and Middle Europe) and *G. versicolor* (ranging from southern Sweden to England, France, Germany, Austria and Poland). The single Nearctic species, *G. io*, is recorded from eastern Canada and northeastern USA (Sabrosky and Arnaud 1965).

List of described species included in *Goniocera*

N   *io* (Aldrich), 1929: 10 (*Cartocometes*). Holotype female, USA: New York, Riverhead (USNM).

P   *montium* (Villeneuve), 1921: 47 (*Actia* (*Euchaetactia*)). Holotype male, France: [Col du] Lautaret (CNC). Holotype examined.

P   *schistacea* Brauer and Bergenstamm, 1891: 354. Holotype female, Austria (not

located).

    syn.   *enigmatica* Villeneuve and Nielsen *in* Nielsen, 1917: 32. Holotype
            female, Denmark: Tisvilde (not located).— Mesnil, 1962: 800.

P   *versicolor* (Fallén), 1820: 19 (*Tachina*). Syntypes, Sweden: Skåne (NRS).

    syn.   *latifrons* (Meigen), 1824: 365 (*Tachina*). Holotype female, Austria
            (lost).— Herting, 1984: 120.
            hartigii (Ratzeburg), 1844: 172 (*Musca* (*Tachina*)). Type, Germany
            (lost).— Herting, 1982: 8.
            ludibunda (Robineau-Desvoidy), 1850: 195 (*Ceromya*). Syntypes,
            France (lost).— Herting, 1974: 18.

<div align="center">

Genus *Proceromyia* Mesnil

Figs. 2-3, 48-49, 73-74, 108-109, 146.

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Proceromyia Mesnil, 1957: 35 (as subgenus of *Ceromya*). Type-species, *Ceromya* (*Proceromyia*)
    macronychia Mesnil, 1957 (monotypy).
Nipponoceromyia Mesnil and Shima, 1978: 324. Type-species, *N. pubioculata* Mesnil and Shima, 1978
    (original designation). **New synonymy.**

Recognition

The two described species of *Proceromyia* are only recorded from Japan and the
Kuril Islands. One, *P. pubioculata*, is markedly autapotypic in external head
features, differing from other siphonines in having a densely haired eye and 8-12
frontal setae (Fig. 3). The other species, *P. macronychia*, is less distinctive and
easily mistaken externally for a *Ceromya* species (head shown in Fig. 2). Both
species share externally the following unique combination of character states (*cf.*
Table 1): narrow vertex (apparently unique, but not quantitatively assessed in this
study), prosternum bare (rare among siphonines), fore tibia with preapical *ad* seta
subequal in length or longer than *d* seta (as in *Entomophaga* species and several
other species), large tarsal claws (only as large in some *Siphona s.s.* species), wing
vein R_{4+5} setulose between base and crossvein *r-m* and other veins bare, and anal
vein not extended to wing margin.

Features of the male genitalia, particularly shape of sternum 5 (Figs. 48-49),
pregonite (Figs. 73-74) and distiphallus (Figs. 108-109) are also diagnostic for the
genus, though the latter two structures closely resemble those in the sister genus
Entomophaga (Figs. 75-76 and 110-111). *Proceromyia* species are distinguished
externally from those of *Entomophaga* by their short aristomere 1 (*cf.* Figs. 2-3 and
4-5), bare prosternum and larger tarsal claws.

Key to adults of *Proceromyia* species

(See section entitled "Review of major keys to genera and subgenera of the
Siphonini" for information about how other authors have keyed (and classified) the
following species.)

1.   Eye densely haired; 8-12 frontal setae (Fig. 3, eye hairs not shown) (Japan)..........*Proceromyia pubioculata* Mesnil & Shima

1'   Eye almost bare; five frontal setae (Fig. 2) (Japan and Kuril Islands)................................. *Proceromyia macronychia* Mesnil

Description

(Note: female of *P. pubioculata* unknown.)

Length: 3.0-5.5mm.

Head (Figs. 2-3).— (Head of *P. pubioculata* also shown in Mesnil and Shima 1978, fig. 10.) Generally five frontal setae in *P. macronychia*, 8-12 in *P. pubioculata*, rather fine in both. Proclinate orbital setae thin but average length, subequal in most specimens. Eye almost bare (*P. macronychia*) or densely haired (*P. pubioculata*). Eye of male and female subequal, medium-large, 0.78-0.84 head height. Flagellomere 1 of male short to medium-short, 0.34-0.43 head height; shape average in width; not bifid. Flagellomere 1 of female usually slightly smaller than in male. Aristomere 1 short. Aristomere two 1.5-3X longer than wide. Aristomere 3 almost bare, slightly short to normal length, evenly tapered to tip or abruptly narrowed on apical two-thirds. Clypeus U-shaped in *P. macronychia*, not examined in *P. pubioculata*. Palpus short to medium, clavate. Proboscis with prementum short, labella padlike.

Thorax.— Prosternum bare. Lower proepimeral seta weak, not directed downward. Katepisternum bare anterior to mid coxa. Lower katepisternal seta shorter than upper anterior seta. Three postsutural dorsocentral setae. Upper part of anepisternum with single setula in *P. macronychia*, with three setulae in single examined specimen of *P. pubioculata*. Fore tibia with preapical *ad* seta subequal to or longer than *d* seta. Mid tibia with one *ad* seta. Tarsomeres normal in size; claws large. Wing: CuA_1 with distal portion 0.24-0.32 length of proximal portion (*i.e. dm-cu* near wing margin; mean 0.27); anal vein not extended to wing margin. Wing setulae: R_1 bare dorsally and ventrally; R_{4+5} setulose between base and *r-m*; CuA_1 bare.

Abdominal terga 1-5.— Abdomen ovoid in shape. T_{1+2} without median marginal setae; lateral marginal setae strong. T_3-T_5 average or with lateral discal setae on one or more segments.

Male genitalia (Figs. 48-49, 73-74, 108-109).— S_5 (Figs. 48-49) little varied, posterior margins of processes obtusely angled; apical lobe slightly differentiated; median lobe rounded, relatively unmodified; processes moderately setulose. T_6 forming single, broad, dorsally continuous sclerite. Ejaculatory apodeme with fan-shaped portion slightly wider to about 1.5X wider than hypandrial apodeme. Pregonite (Figs. 73-74) in profile smoothly curved anteriorly and more or less pointed apically, with small spines along anterolateral ridge. Epiphallus small in *P. pubioculata*, absent from *P. macronychia*. Distiphallus (Figs. 108-109) with posterior margin partially reduced, laterally incised, anterior margin reduced except for long, spined anterolateral arm; apex broader than long in ventral view. Postgonite apically broad and turned outward. Surstylus average length, broadened at midlength, straight; basally free from epandrium. Cerci rather short (*P. macronychia*) to average length (*P. pubioculata*), smoothly curved at midlength; moderately setose on basal half.

Examined male genitalia of: *P. macronychia* and *P. pubioculata* (latter shown in Mesnil and Shima 1978, fig. 11).

Female genitalia (Fig. 146).— (Only *P. macronychia* examined.) Short. S_6 with short hairs. T_6 distinctly developed, enclosing spiracles of segment 6; narrowly discontinuous dorsally. S_7 with long anterior apodeme; without posteromedial keel. T_7 present as two lateral sclerites; spiracles of segment 7 displaced anteriorly and enclosed in posterior margin of T_6. S_8 distinctly developed, haired. T_{10} present as small median sclerite.

Examined female genitalia of: *P. macronychia*.

Hosts. Unknown.

Phylogenetics

Mesnil described *P. macronychia* in 1957 (p. 35) as a new species in new subgenus *Ceromya (Proceromyia)*, basing the new taxon primarily on the presence of large claws and narrow vertex. At that time *Ceromya s.l.* was recognized as a

siphonine genus in which the anal vein did not extend to the wing margin and from which the derived features of *Actia* and *Goniocera* were lacking.

Mesnil later completely revised the Palearctic *Ceromya* species (1963a: 829), and recognized two primary divisions within the genus: *Ceromya (Ceromya)* characterized by wing vein R_{4+5} setulose from base to beyond crossvein *r-m*, and both *C. (Proceromyia)* and *C. (Stenoparia)* characterized by vein R_{4+5} not setulose beyond *r-m*. I discuss here the monophyly of Mesnil's *C. (Proceromyia)* - status of *C. (Stenoparia)* and placement of its type species *C. monstrosicornis* are discussed in the Phylogenetics section of *Ceromya s.s.*, while the other *C. (Stenoparia)* species recognized by Mesnil, *C. nigrohalterata*, is placed in *Entomophaga* and discussed in the Phylogenetics section of that genus.

The second species here included in *Proceromyia* is a siphonine of unusual appearance, *P. pubioculata*. This species was described in its own genus, *Nipponoceromyia* Mesnil and Shima (1978), primarily because of its uniquely haired eye and numerous frontal setae (Fig. 3). The authors commented that *P. pubioculata* seemed related to *Proceromyia macronychia* (1978: 325), citing as evidence the shared possession of weak proclinate orbital setae, narrow vertex and short distal section of wing vein CuA_1. I doubt that the first character state is uniquely shared by these two species, the last certainly is not, but the narrow vertex might be a synapotypy of these species. Both species also have unusually large tarsal claws. The male genitalia of *Proceromyia macronychia* and *Nipponoceromyia pubioculata* were apparently not compared by Mesnil and Shima, but corroborate their phylogenetic hypothesis and as discussed below provide better evidence for a sister species relationship between these species.

Similarities in the male genitalia of *Proceromyia macronychia* and *Nipponoceromyia pubioculata* belie the external differences between these species, leading to the conclusion that the autapotypic features of *N. pubioculata* are the result of divergence from a more *P. macronychia*-like ancestor. In support of this are the remarkable similarities in male sternum 5 (Figs. 48-49), pregonite (Figs. 73-74) and distiphallus (Figs. 108-109) - similarities which also attest to a close relationship with *Entomophaga* (see the Phylogenetics section of that genus and the Evolution chapter for a discussion of these intergeneric relationships). Given the general external similarities between *P. macronychia* and *P. pubioculata* (listed in Recognition section) and diverse shapes of male genitalia among siphonines in general, I regard the shared similarities in male genitalia of these two species as synapotypies. I propose the following classification to reflect this hypothesized relationship between *P. macronychia* and *N. pubioculata*: *N. pubioculata* is moved to *Proceromyia*, and *Proceromyia* is ranked at the generic level because of its sister group relationship with *Entomophaga*, and its lack of known synapotypies with *Ceromya*. Both *Proceromyia* and *Nipponoceromyia* were ranked as monobasic genera by Herting (1984: 121-2) before the male genitalia of the two included species were compared (in contrast, Andersen 1983 placed *Proceromyia* as a

synonym of *Ceromya* and did not study *Nipponoceromyia pubioculata*). It seems appropriate to modify Herting's classification of these two species by combining them under one generic name now that their genitalic features are known to be so similar.

Geographic distribution

The known ranges of the two included species are very limited: *P. macronychia* was described from Hokkaido, Japan, and has since been recorded from the Kuril Islands, USSR (Richter 1976b). *P. pubioculata* is only known from male specimens collected from Honshu Island, Japan.

List of described species included in *Proceromyia*

P   *macronychia* (Mesnil), 1957: 35 (*Ceromya* (*Proceromyia*)). Holotype male, Japan: Hokkaido, Obihiro (CNC). Holotype examined.

P   *pubioculata* (Mesnil and Shima), 1978: 325 (*Nipponoceromyia*). Holotype male, Japan: Honshu, Kawaragoya (BLKU). Paratype examined. **New combination**.

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Genus *Entomophaga* Lioy

Figs. 4-5, 50-51, 75-76, 110-111, 147.

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Entomophaga Lioy, 1864: 1332. Type-species, *Tachina exoleta* Meigen, 1824 (by designation of Coquillett, 1910: 538).

Recognition

Entomophaga comprises two described European species, *E. nigrohalterata* and *E. exoleta*. The former is commonly collected while the latter is known from very few specimens. A diagnostic combination for these species is the possession of an elongate aristomere 1 (Figs. 4-5), fore tibia with preapical *ad* seta subequal in length or longer than *d* seta, wing vein R_{4+5} setulose between base and crossvein *r-m* and other veins bare, and anal vein not extended to wing margin (*cf*. Table 1). In addition, features of the male genitalia are distinctive, and are similar only to the male genitalia of the externally very different appearing *Proceromyia* species (*cf*. head profiles in Figs. 2-5, sternum 5 in Figs. 48-51, pregonite in Figs. 73-76 and distiphallus in Figs. 108-111).

Entomophaga exoleta has been considered an *Actia* species by some authors because of its row of hairs on the katepisternum anterior to the mid coxa (as in Fig. 33), but is clearly misplaced there based on other features (see Phylogenetics section and Evolution chapter). Likewise, *E. nigrohalterata* has been mistaken for a *Ceromya* species because its phylogenetically important character states have been misinterpreted.

Key to adults of *Entomophaga* species

(See section entitled "Review of major keys to genera and subgenera of the Siphonini" for information about how other authors have keyed (and classified) the following species.)

1.   Three postsutural dorsocentral setae; katepisternum with row of hairs directly anterior to mid coxa, extended upward almost to lower katepisternal seta (as in *Actia* spp., Fig. 33); male sternum 5 U-shaped, apical lobe distinctly differentiated (Fig. 50); pregonite spined along anterolateral margin (Fig. 75); distiphallus with lateral margin markedly reduced (Fig. 110) (Europe; very rarely collected). *Entomophaga exoleta* (Meigen)

1'.   Four postsutural dorsocentral setae; katepisternum almost bare directly anterior to mid coxa, except for several hairs in posteroventral corner (Fig. 34); male sternum 5 with apical lobe slightly differentiated (Fig. 51); pregonite bare along anterolateral margin (Fig. 76); distiphallus with lateral margin partially reduced (Fig. 111) (Europe; commonly collected)..............................*Entomophaga nigrohalterata* (Vill.)

Description

Length: 3.0-5.0mm.

Head (Figs. 4-5).— Four or five frontal setae, in normal arrangement. Anterior proclinate orbital seta longer than posterior one in *E. exoleta*, setae subequal in length in *E. nigrohalterata*. Eye bare. Eye of male small to medium, 0.63-0.77 head height; eye of female slightly larger than in male. Flagellomere 1 of male medium to medium-long, 0.58-0.66 head height; shape broad to subquadrangular; not bifid. Flagellomere 1 of female slightly smaller than in male. Aristomere 1 elongate, 1.5-5X longer than wide. Aristomere two 3-4X longer than wide. Aristomere 3 almost bare, slightly shorter than average, evenly tapered to tip. Clypeus U-shaped. Palpus long, clavate. Proboscis with prementum short, labella padlike.

Thorax.— Prosternum setulose. Lower proepimeral seta weak, not directed downward. Katepisternum bare (*E. nigrohalterata*) or with row of hairs anterior to mid coxa (*E. exoleta*). Lower katepisternal seta shorter than upper anterior seta. Three (*E. exoleta*) or four (*E. nigrohalterata*) postsutural dorsocentral setae. Upper part of anepisternum with single setula. Fore tibia with preapical *ad* seta subequal to or longer than *d* seta. Mid tibia with one *ad* seta. Tarsomeres normal in size, claws small to medium-large. Wing: CuA_1 with distal portion 0.25-0.43 length of proximal portion (*i.e. dm-cu* near wing margin; mean 0.33); anal vein not extended to wing margin. Wing setulae: R_1 bare dorsally and ventrally; R_{4+5} setulose between base and *r-m*; CuA_1 bare.

Abdominal terga 1-5.— Abdomen ovoid in shape. T_{1+2} without median marginal setae; lateral marginal setae strong. T_3-T_5 average or with lateral discal setae on 1 or more segments.

Male genitalia (Figs. 50-51, 75-76, 110-111).— S_5 with apical lobe of processes slightly differentiated (posterior margins almost transverse, Fig. 51) in *E. nigrohalterata*, distinctly differentiated and posterior margin approximately U-shaped in *E. exoleta* (Fig. 50); median lobe rounded, relatively unmodified; processes moderately setulose. T_6 forming single, broad, dorsally continuous sclerite. Ejaculatory apodeme with fan-shaped portion slightly wider to almost 2.0X wider than hypandrial apodeme. Pregonite in profile smoothly curved anteriorly, pointed apically; either bare (*E. nigrohalterata*, Fig. 76) or spined along anterolateral margin (*E. exoleta*, Fig. 75). Epiphallus present: very short in *E. nigrohalterata*, long and narrow in *E. exoleta*. Distiphallus (Figs. 110-111) with posterior margin partially reduced, laterally incised, anterior margin reduced except for long, spined anterolateral arm; broader than long in ventral view. Postgonite apically broad and turned outward. Surstylus average length, straight (*E. nigrohalterata*) or

curved posteriorly (*E. exoleta*); basally free from epandrium. Cerci rather short, smoothly curved at midlength; moderately setose on basal half.

Examined male genitalia of: *E. exoleta* and *E. nigrohalterata* (latter shown in Andersen 1983, fig. 24).

Female genitalia (Fig. 147).— (Only *E. nigrohalterata* examined.) Short. S_6 with very short hairs. T_6 distinctly developed, enclosing spiracles of segment 6; narrowly discontinuous dorsally. S_7 with long anterior apodeme; slightly keeled posteromedially. T_7 present as two lateral sclerites; spiracles of segment 7 displaced anteriorly to very near or associated with T_6. S_8 absent. T_{10} absent or present as two small sclerites. Examined female genitalia of: *E. nigrohalterata* (also see Andersen 1983, fig. 9).

Hosts.   Unknown.

Phylogenetics

Herting (1975: 4) revised the standard classification of *E. exoleta* and *E. nigrohalterata* by removing the former from *Actia* and the latter from *Ceromya*, and uniting them under a newly defined *Entomophaga* Lioy (*cf*. Mesnil 1963a). Herting based his concept of *Entomophaga* primarily on two characteristics shared by *E. exoleta* and *E. nigrohalterata*: an elongate aristomere 1 and long preapical *ad* seta on fore tibia. The second feature is shown in this study to be shared with related taxa (see Evolution chapter), but the first is accepted here as a synapotypy of *Entomophaga*, though not unique to the genus (Table 1).

Recently Andersen (1983: 12) reviewed the Old World Siphonini and re-assigned *E. exoleta* to *Actia* and *E. nigrohalterata* to *Ceromya*. Andersen returned *E. exoleta* to *Actia* because he considered its row of katepisternal hairs to be clear evidence of its membership in *Actia*. He interpreted the elongate aristomere 1 of *E. exoleta* and *E. nigrohalterata* as autapotypies of each species, consequently returning the latter to *Ceromya* because "it does not differ significantly from other *Ceromya* species in external characters" (1983: 12). However, Andersen noted that the male and female genitalia of *E. nigrohalterata* were different from the *Ceromya*-type.

Andersen's classification of the two species here placed in *Entomophaga* and *Proceromyia* was based on external characters, since only the genitalia of *E. nigrohalterata* were examined. I hypothesize that characteristics of the male genitalia of the four *Entomophaga* and *Proceromyia* species indicate that these species form a monophyletic lineage, based on shape of the pregonite (Figs. 73-76) and distiphallus (Figs. 108-111), which are derivable from a common groundplan and lack synapotypies with the *Actia* and *Ceromya* lineages. The two *Proceromyia* species are not only remarkably similar in male genitalic features (Figs. 48-49, 73-74, 108-109) but share unique external similarities as well, so are certainly sister species. The male genitalia of *Entomophaga* species are more equivocal: they clearly indicate a close relationship with *Proceromyia*, but not a sister species relationship between *E. exoleta* and *E. nigrohalterata*. However, given the general external similarities between *E. exoleta* and *E. nigrohalterata*, particularly head habitus (Figs. 4-5) and derived state of aristomere 1, these species most probably form a monophyletic group. If these external similarities are not synapotypies then

Entomophaga might be paraphyletic with respect to *Proceromyia* (*i.e.* either *E. exoleta* or *E. nigrohalterata* being more closely related to the *Proceromyia* lineage than to its congener).

Features of the male genitalia of *E. exoleta* not only corroborate its placement in the *Entomophaga+Proceromyia* lineage, but provide the best evidence for removing this species from *Actia*. *Actia* species share the synapotypies of a more or less V-shaped sternum 5 (Figs. 58-59) and apically spinose pregonite (Figs. 85-86), and these states are lacking from *E. exoleta*. It is concluded that the row of katepisternal hairs that are found (among siphonines) only in *E. exoleta* and most *Actia* species is the result of convergence; convergence certainly accounts for the presence of this row of hairs in *Actia* and some non-siphonine tachinids. *E. exoleta* also has one seta on the upper portion of the anepisternum while almost all *Actia* species have two (*cf.* Figs. 31 and 32).

E. nigrohalterata has not been shown to share any synapotypies with *Ceromya*, either here or by previous authors. Spinules on the membranous portion of the pregonite in most *Ceromya s.s.* species, here considered a synapotypy of *Ceromya s.s.*, are absent from *E. nigrohalterata*. Further research is needed to resolve relationships within *Ceromya s.l.*, and will not only provide information relevant to the placement of *E. nigrohalterata*, but to other species of *Entomophaga* and *Proceromyia* as well.

Adult females of *E. nigrohalterata* are atypical in their lack of a sclerotized abdominal sternum 8 (Fig. 147). Study of the female genitalia of *E. exoleta* has not yet been possible, but if sternum 8 is lacking then a sister species relationship between *E. exoleta* and *E. nigrohalterata* would be corroborated (otherwise this loss might be autapotypic of *E. nigrohalterata*).

Similar in some respects to the species of *Entomophaga* is *Ceromya monstrosicornis*. Its placement is discussed in the Phylogenetics section of *Ceromya s.s.*

Geographic distribution

Entomophaga exoleta is a rarely collected species, recorded from a few localities in France (type locality, and a female in SMNS), Hungary (Andersen, pers. comm.) and England (Crosskey 1976b). *E. nigrohalterata* is a relatively common species in Europe, with records from England, Belgium, Denmark, Germany, Poland, Austria and Switzerland (Mesnil 1963a, Herting 1967b, 1984, Draber-Mońko 1978, 1981). *E. exoleta* and *E. nigrohalterata* are at least narrowly sympatric, with the former slightly more southern in distribution.

List of described species included in *Entomophaga*

P   *exoleta* (Meigen), 1824: 353 (*Tachina*). Syntypes, France: Provence (MNHN).
      syn.   *anicula* (Meigen), 1824: 409 (*Tachina*). Holotype female, Europe

(MNHN).— Herting, 1975: 2.

P   *nigrohalterata* (Villeneuve), 1921: 45 (*Actia*). Holotype male, Denmark (CNC). Holotype examined.

    syn.   *articulata* (Stein), 1924: 131 (*Actia*). Syntypes, Copenhagen, Denmark and Löbauer Berg, German Democratic Republic (ZMUC; not located, possibly lost).— Lundbeck, 1927: 465.

        sufferta (Villeneuve), 1942b: 133 (*Actia*). Holotype male, Germany: no locality given (CNC).— Herting, 1981: 8. Holotype examined.

Genus *Ceromya* Robineau-Desvoidy *sensu lato*
Figs. 6-7, 35, 37, 39-40, 52-57, 77-84, 112-116, 138, 148-150, 157, 159.

Note about classification of *Ceromya s.l.* species

No known features are clearly interpretable as synapotypic of *Ceromya s.l.*, and as a result the monophyly of this diverse and cosmopolitan genus has not been positively established. However, features of the male genitalia suggest that *Ceromya s.l.* comprises two monophyletic lineages. These are here called *Ceromya s.s.* (including type species *C. bicolor*) and the *C. silacea* species group (an informal species group in which *C. silacea* is the most derived species and has the oldest name), and are treated individually throughout this paper.

The unusual division of *Ceromya s.l.* into two categories of different rank is adopted for practical and nomenclatural reasons. Firstly, male genitalia were not studied in all *Ceromya s.l.* species, so characterization of the lineages may be incomplete, as well as assignment of described species to the *C. silacea* species group. Secondly, recognition of the *C. silacea* species group as a subgenus or genus would require erection of a new genus-group name, which is premature on the basis of available evidence. *Ceromya s.s.* could equally well be called the *C. bicolor* species group, but the former designation was chosen to clearly identify the group that would be called *Ceromya* if the *C. silacea* species group is later removed from *Ceromya s.l.*

Recognition

Ceromya s.l. belongs to the group of siphonines in which the anal vein is not extended to the wing margin (Fig. 21). This characteristic separates all known *Ceromya s.l.* species from species of *Peribaea* and *Siphona s.l.* Additionally, the lower katepisternal seta is shorter than the upper anterior one in all but a very few *Ceromya s.l.* species (Fig. 31) while subequal in length or longer in most *Peribaea* and *Siphona s.l.* species (Fig. 32; see Table 1).

New World species of *Ceromya s.l.* are easily separable from other New World siphonines by the following combination of states: anal vein not extended to wing margin (Fig. 21), absence of row of hairs on katepisternum (Fig. 34; row present in all New World *Actia* species, Fig. 33) and only one *ad* seta on mid tibia (Fig. 37;

row of *ad* setae in *Goniocera io*, the only New World *Goniocera* species).

Four Old World genera - *Goniocera*, *Actia*, *Entomophaga* and *Proceromyia* - are characterized along with *Ceromya s.l.* by an anal vein not extended to the wing margin. All *Goniocera* species have a row of *ad* setae on the mid tibia (0-1 seta in *Ceromya s.l.* species, as in Figs. 37-38) and are separable from *Ceromya s.l.* species by this feature. The diagnosis given above for New World *Ceromya s.l.* species will not separate Old World members of this taxon from species of *Entomophaga* or *Proceromyia*, or several *Actia* species. It is therefore necessary to diagnose Old World *Ceromya s.l.* species by the presence of at least six of the following seven states: 0-1 anepisternal setula, lower katepisternal seta shorter than upper anterior one, katepisternum lacking row of hairs, fore tibia with short preapical *ad* seta, mid tibia with 0-1 *ad* seta, wing vein R_{4+5} setulose beyond crossvein *r-m* and anal vein not extended to wing margin. Similarities and differences among Old World *Ceromya s.l.* species and Old World *Actia*, *Entomophaga* and *Proceromyia* species are discussed below.

Most Old World *Actia* species are distinguishable from *Ceromya s.l.* species by presence of a row of katepisternal hairs (Fig. 33), but a very few Old World *Actia* species lack this row of hairs and must be recognized by other features (externally by presence of two anepisternal setulae, though characteristics of the male genitalia provide the best means by which to recognize *Actia* species - see Recognition section of *Actia*).

The four species of *Entomophaga* and *Proceromyia* share two states which in combination distinguish them from *Ceromya s.l.* species: fore tibia with preapical *ad* seta subequal in length or longer than *d* seta (only shared with two *Ceromya* species: Nepal sp. 1 and Australia sp. 3) and wing vein R_{4+5} not setulose beyond crossvein *r-m* (same in three *Ceromya* species: *C. cephalotes*, *C. monstrosicornis* and *C. natalensis*). Features of pregonite and distiphallus are also unique to the *Entomophaga+Proceromyia* lineage.

Male genitalic features of *Ceromya s.l.* species are discussed in the Recognition sections of *Ceromya s.s.* and *C. silacea* species group. The possible monophyly of *Ceromya s.l.* is discussed in the Evolution chapter.

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Ceromya Robineau-Desvoidy *sensu stricto*
Figs. 6-7, 39-40, 53-57, 77-83, 113-116, 138, 149-150, 157.

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Ceromya Robineau-Desvoidy, 1830: 86. Type-species, *C. testacea* Robineau-Desvoidy, 1830 (by designation of Coquillett, 1910: 520) = *Tachina bicolor* Meigen, 1824.

Ceromyia. Variant spelling of *Ceromya*.

Polychaetoneura Walton, 1914: 90. Type-species, *P. elyii* Walton, 1914 (original designation) = *Thryptocera americana* Townsend, 1892. Recent synonymy by Wood (1987: 1239) in key to Nearctic tachinid genera.

Xanthoactia Townsend, 1919: 585. Type-species, *Lasioneura palloris* Coquillett, 1895 (original designation). Recent synonymy by Wood (1987: 1239) in key to Nearctic tachinid genera.

Stenoparia Stein, 1924:*S. (Siphona)* 128. Type-species, *S. monstrosicornis* Stein, 1924 (monotypy).

Schizoceromyia Townsend, 1926b: 542. Type-species, *Schizotachina fergusoni* Bezzi, 1923 (original designation).

Actinactia Townsend, 1927: 248. Type-species, *A. lutea* Townsend, 1927 (original designation). **New synonymy.**

Schizactiana Curran, 1927b: 356 (as subgenus of *Actia*). Type-species, *Actia* (*Schizactiana*) *valida* Curran, 1927 (original designation).

Pseudactia Malloch, 1930b: 124 (as subgenus of *Actia*). Type-species *Actia* (*Pseudactia*) *hirticeps* Malloch, 1930 (monotypy).

Recognition

Features of the male genitalia provide the only means for placing *Ceromya s.l.* species into *Ceromya s.s.* or the *Ceromya silacea* species group. The following characteristics of the male genitalia distinguish species of *Ceromya s.s.* from those of the *C. silacea* species group: pregonite with enlarged membranous area anteriorly, with tiny spinules in most species (Figs. 39-40, 77-83; similar in *Goniocera io* (Fig. 71), otherwise unique to *Ceromya s.s.* species); and distiphallus without infolded, sclerotized structure posteriorly (Figs. 113-116; *cf. C. silacea*, Fig. 112).

External features of specimens of most described *Ceromya s.l.* species were examined during this study, but male genitalia were examined in specimens of only a portion of these species (as listed in descriptions of male genitalia of *Ceromya s.s.* and *C. silacea* sp. grp.). Possibly a complete study of the male genitalia of all species listed in *Ceromya s.s.* will reveal several species that should be reassigned to the *C. silacea* species group. The evidence available at this time is insufficient to permit a thorough reclassification of *Ceromya s.l.* species into *Ceromya s.s.* and *C. silacea* species group.

Description

Length: 3.0-6.0mm.

Head (Figs. 6-7).— Five frontal setae in most species, three or four in a very few; normal arrangement. Anterior proclinate orbital seta longer than posterior one in most species. Eye size of male medium-small to large, 0.68-0.86 head height; eye of female slightly smaller to slightly larger than in male, in most species eye size of sexes subequal. Flagellomere 1 of male markedly varied in length, 0.38-0.80 head height; shape from linear to subquadrangular, bifid in *C. fergusoni*, *C. invalida* and *C. valida*, normal in others. Flagellomere 1 of female smaller than in male; not bifid. Aristomere 1 short. Aristomere two 1.5-6X longer than wide in species with normal antenna, up to 10X in species with bifid flagellomere 1. Aristomere 3 short and thickened to near tip, to long and evenly tapered; almost bare, micropubescent, or rarely short plumose. Clypeus U-shaped in most species, narrow and enclosed in membrane in a few. Palpus short in most species, medium to long in a few; enlarged apically in females of a few species; clavate. Proboscis with prementum short, labella padlike (labella very slightly lengthened in *C. luteicornis*).

Thorax.— Prosternum setulose in most species, bare in a very few. Lower proepimeral seta weak, not directed downward except in a very few species (though not long as in *Peribaea* species). Katepisternum bare anterior to mid coxa. Lower katepisternal seta much shorter than upper anterior seta in most species, slightly shorter or subequal to it in two closely related species: *C. flaviseta* and *C. ontario*. Three or four postsutural dorsocentral setae. Upper part of anepisternum with single setula. Fore tibia with preapical *ad* seta much shorter than *d* seta in almost all species, known to be as long as *d* seta only in Nepal sp. 1 and Australia sp. 3. Mid tibia without *ad* seta in *C. fergusoni*, one *ad* seta in other species. Tarsomeres normal in size in most species, with tarsomere 5 of fore leg elongate and broadened in female of several species; tarsomere 5 of all legs elongate and dilated in female of Australia sp. 3; claws short in most species, medium

in a few. Wing: CuA_1 with distal portion 0.24-0.67X length of proximal portion (mean 0.40); anal vein not extended to wing margin. Wing setulae: R_1 dorsally bare, or distally or entirely setulose, ventrally bare or distally setulose; R_{4+5} setulose from base to beyond r-m in most species, not beyond r-m in $C.$ $cephalotes$, $C.$ $natalensis$ and $C.$ $monstrosicornis$. CuA_1 bare or setulose, with basal section setulose in $C.$ $americana$ complex, $C.$ $languidula$, Brazil spp. 1 and 4 (bare in other siphonines).

   $Abdominal$ $terga$ 1-5.— Abdomen ovoid in shape in almost all species, slightly elongate in a very few. T_{1+2} without median marginal setae; lateral marginal setae absent to strong. T_3-T_5 average in most species, with weak lateral discal setae (T_3-T_5) and/or extra pair of lateral marginal setae (T_3 and T_4 only) in a few.

   $Male$ $genitalia$ (Figs. 39-40, 53-57, 77-83, 113-116, 138).— S_5 markedly varied, inner (or posterior) margins of processes obtusely angled (Fig. 55) to transverse (Fig. 57), in most species U-shaped (Figs. 53-54, 56); apical lobe usually undifferentiated (Fig. 57) to narrowly pointed, in a very few species distinctly differentiated and apically curved inward (Fig. 56); median lobe markedly varied, from rounded (Figs. 55-56) or elongate (Fig. 53) to flattened plate of varied forms (Fig. 54; rarely similar to shape in $Goniocera$), and with or without accessory lobe; processes sparsely to densely setulose. T_6 varied from two very small lateral sclerites to a single, broad, dorsally continuous sclerite. Ejaculatory apodeme with fan-shaped portion 0.5-1.5X width of hypandrial apodeme. Pregonite in profile extremely varied: membranous anterior portion of pregonite enlarged in most species and usually with spinules anterolaterally (Figs. 39-40, 79-83; these often tiny and visible only at higher magnifications, 100-400X); in one species ($C.$ $lutea$, Fig. 83) pregonite elongate and curved posteriorly (unique within the Siphonini); in one Old World group pregonite ring-shaped and spinules borne anteriorly on sclerotized portion (Fig. 78). Epiphallus present or absent. Distiphallus (Figs. 113-116) extremely varied: in most species anterior margin incised, posterior margin entire in $C.$ $lutea$ (Fig. 116) and Nepal sp. 1, at least partially incised in other species, in profile distiphallus laterally incised to varied degrees in most species (Figs. 114-116), lateral margin entire apically in a few (Fig. 113). Postgonite large, apically rounded, curved ventrally, or bilobed. Surstylus short to long, thin to broad (Fig. 138), straight or curved posteriorly; with long hairs along length in $C.$ $languidula$ (and in $C.$ $varichaeta$ of $Ceromya$ $silacea$ sp. grp.); basally fused with epandrium in most species (Fig. 138), free in others. Cerci short to average length, deeply inflexed at midlength in some species (Fig. 138), smoothly curved in others; moderately to densely (Fig. 138) setose on basal half.
Examined male genitalia of: $C.$ $amblycera$, $C.$ $americana$ complex, $C.$ $cornuta$, $C.$ $flaviceps$, $C.$ $flaviseta$, $C.$ $invalida$, $C.$ $languidula$, $C.$ $lavinia$, $C.$ $lutea$, $C.$ $natalensis$, $C.$ $ontario$, $C.$ $palloris$, $C.$ nr. $punctipennis$, Australia spp. 1-2,5, Brazil spp. 1,3-4, Chile spp. 1-2, Mexico spp. 2-5, Nepal sp. 1, New Guinea spp. [numbered by Shima] 4,6,11,15,18, Peru sp. 1 and U.S. sp. 1. Examined published figures of: $C.$ $bicolor$ (Andersen 1983, fig. 23) and $C.$ $pruinosa$ (Shima 1970c, figs. 3f, 6).

   $Female$ $genitalia$ (Figs. 149-150).— Short to relatively long and extensible. S_6 with short to average length hairs, though species with short hairs usually sparsely haired on most of sternite with longer row of hairs along posterior margin. T_6 varied from two small lateral sclerites to distinctly developed and narrowly discontinuous dorsally; spiracles of segment 6 near or enclosed within anteroventral portion of T_6. S_7 without anterior apodeme in most species, with apodeme in a few; a few species slightly to (rarely) sharply keeled posteromedially. T_7 absent from a few species, present as two small to large lateral sclerites in most species; spiracles of segment 7 in most species in membrane between segments 6 and 7, in a few species enclosed within T_6 or near T_7. S_8 distinctly developed, haired. T_{10} absent to distinctly developed as a median plate or two sclerites.
Examined female genitalia of: $C.$ $americana$ complex, $C.$ $bicolor$ (Andersen 1983, fig. 10), $C.$ $cornuta$, $C.$ $lavinia$, $C.$ $lutea$, $C.$ $ontario$, Australia sp. 3 and Nepal sp. 4.

Taxonomic changes

   $Lectotype$ $designation$ for $Ceromya$ $cibdela$ $(Vill.)$.— $Ceromya$ $cibdela$ was described in $Actia$ by Villeneuve in 1913 from an unspecified number of specimens collected from Oshogbo, Nigeria, during October and November of 1910. While studying siphonine collections in the BMNH and CNC, I found a specimen in each labelled as the type of $C.$ $cibdela$ and bearing appropriate locality data. Each specimen bears a type label characteristic of the institution: a round, red-bordered "Type" label on the BMNH specimen, and a red, rectangular "TYPE" label on the

CNC specimen (of the sort used in the CNC to denote types in the Mesnil collection). Both additionally have attached a Villeneuve determination label with the designation "Typ.". Both specimens fit Villeneuve's brief description of the species and by all indications are syntypes (no holotype designation was published). They are not, however, conspecific. The CNC specimen belongs to *Ceromya* and agrees with the current interpretation of *C. cibdela* (Mesnil 1954, 1963a, Crosskey 1976a), while the BMNH specimen belongs to *Siphona (Aphantorhaphopsis)*. To retain *C. cibdela* in its current usage I hereby designate the CNC specimen as lectotype. The condition of the CNC specimen also favors its selection as lectotype because it is a male in good condition while the BMNH specimen lacks its abdomen.

Notes about Ceromya fergusoni Bezzi and two related nominal species.— Three named species of *Ceromya* from eastern Australia have flagellomere 1 bilobed: *C. fergusoni* (Bezzi 1923b; type-species of *Schizoceromyia*), *C. valida* (Curran 1927b; type-species of *Schizactiana*) and *C. invalida* (Malloch 1930a). These are unquestionably at least closely related, and as discussed below, perhaps conspecific. I dissected a male paratype (USNM) of *C. invalida*, and the presence of spinules distally on the membranous portion of the pregonite confirms its placement in *Ceromya s.s.*

As noted by Crosskey (1973: 137), the type of *C. fergusoni* is missing. Arnaud (1982) cites a paratype in MCSN, but this is in error. The MCSN specimen (examined by me in 1986) bears a collection label of "Sydney, 3.12.23 [December 3, 1923], Health Dept.", and stands in the MCSN collection under the label "*Schizotachina fergusoni* parat. Bezzi". Bezzi did not name a paratype, and his paper describing the species was read on November 28, 1923, about a week before the "paratype" was collected. The specimen is nonetheless important, for reasons given below.

Two characters given by previous authors separate *C. fergusoni, C. valida* and *C. invalida*. One is length of aristomere 2: in the description of *C. fergusoni* it is much longer than length of aristomere 3, in holotype of *C. valida* the articles are subequal in length, and in holotype of *C. invalida* it is slightly more than half length of aristomere 3. The second diagnostic character is presence or absence of an *ad* seta on mid tibia (character 24). *C. fergusoni* is cited as lacking this seta, it is long in the type of *C. valida* and short though stout in type of *C. invalida*. In all other respects the three named species seem not to differ significantly.

Malloch (1930a) knew about both Bezzi's *C. fergusoni* and Curran's *C. valida* when he described *C. invalida*, but finding Curran's description lacking information about the mid tibial *ad* seta, he divided all his material between *C. fergusoni* and *C. invalida*. Malloch apparently did not see any specimens with an aristomere 2 subequal in length to aristomere 3, as decribed for Curran's *C. valida*.[1]

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[1]The labelled holotype of *C. valida* agrees in all respects with its description, but was collected from

I strongly suspect that the character states used to separate the three nominal species are unreliable within this species complex. Length of aristomere 2 is subject to some variation in some other siphonines, particularly those in which it is elongate. Under different circumstances, I would consider the mid tibial *ad* seta as reliable, but several factors suggest it may not be here. Firstly, Malloch's (1930a) specimen's of "*C. fergusoni*" and "*C. invalida*" were collected from the same locality (Sydney), and between the same months (Sept. to Dec.). Secondly, the MCSN specimen identified (by Bezzi?) as *C. fergusoni* lacks the mid tibial *ad* seta as described for that species, but has an aristomere 2 as described for *C. invalida* (also note that this specimen is labelled similarly to the specimens of "*C. fergusoni*" and "*C. invalida*" studied by Malloch). Thirdly, the types of the three nominal species vary in relative length of the mid tibial *ad* seta, suggesting a pattern of intraspecific variability. Fourthly, a BMNH specimen from South Australia has an aristomere two 0.8X length of aristomere 3 and a long mid tibial *ad* seta, placing it closest to *C. valida*, or by Malloch's criteria in *C. invalida*.

I have not examined enough material to firmly establish the conspecificity of the three nominal species discussed above. Neither have I examined the male genitalia of specimens of all three forms to determine if there are genitalic differences among them. Also the correlation between aristomere 2 length and presence/absence of a mid tibial *ad* seta needs to be studied to determine if these characteristics are distributed as uniformly as suggested by Malloch. The evidence now available casts doubt on the correctness of recognizing all three named species as valid species, but I reserve any change in nomenclature until more specimens can be examined and my above concerns addressed.

Hosts

Ceromya s.s. species mostly parasitize Macrolepidoptera, without apparent preference for a particular family (Table 2). A single record for a rearing from a tenthredinid for *Ceromya bicolor* (a common European species also recorded from the Arctiidae and Lasiocampidae) is, if accurate, the only known record of a siphonine parasitizing a hymenopteran.

Phylogenetics

Species of *Ceromya s.s.* are not known to possess any synapotypic character states externally. The group, in addition to members of the *C. silacea* species group, is defined externally by the lack of derived features found in other siphonine lineages (see Recognition section of *Ceromya s.l.*), and *Ceromya s.s.* species are only separable from species of the *C. silacea* species group by features of the male

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[1](cont'd) Palmerston on Sept. 1908 by Lichtwardt, and not (as cited by Curran) collected from Palmerston in 1910 by Fred P. Dodd. There is no other indication that this specimen is not the one selected by Curran as holotype of this nominal species.

genitalia.

Though members of *Ceromya s.s.* do not share known synapotypies externally, one derived characteristic of the male genitalia suggests the group is monophyletic, *i.e.* the more or less enlarged membranous area on the anterior surface of the pregonite, which in most *Ceromya s.s.* species is partially covered with tiny spinules (Figs. 39-40 and 77-83; in some species these spinules are only visible at magnifications of 100X-400X). These spinules are a derived state within the Siphonini, and so far as known are only present in *Ceromya s.s.* species and *Goniocera io.* The phylogenetic significance of this apotypic state in *G. io* is discussed in the Evolution chapter, though for the purposes of this discussion the state is interpreted as independently derived in *G. io* and *Ceromya s.s.*

The size and number of spinules on the pregonite of *Ceromya s.s.* species varies from species to species, and they are entirely absent from a few (*cf.* Figs. 77-83). Species which lack spinules are, with rare exceptions (as discussed below), assignable to species groups which possess them (for example, the pregonite is bare in *C. flaviceps* and spinulose in several closely related species), so presence of spinules is here interpreted as the groundplan condition, or is an underlying synapotypy (as defined in Evolution chapter), of *Ceromya s.s.* Several *Ceromya s.s.* species show modification from the simple spinulose condition, such as New Guinea sp. 6 (Fig. 78) and Brazil sp. 3 (Fig. 82), but the pregonite of these species is traceable to the primitive condition through species with intermediate states. More specifically, the pregonite of certain species suggests that the ring-shaped pregonite of New Guinea sp. 6 is derivable from a bilobed pregonite of a *C. flaviceps*-like ancestor, and the enlarged spines on the pregonite of Brazil sp. 3 are derivable from an ancestor with a spinulose condition similar to Mexico sp. 5 (Fig. 81; note that the spined condition of the pregonite in Brazil sp. 3 is distinctly different from the *Actia*-type, Figs. 85-86).

The pregonite of *C. lutea* (Fig. 83) is unique in curving posteriorly. No other siphonine is known to share this condition, and along with the derived shapes of its male sternum 5 (Fig. 57) and distiphallus (Fig. 116), this seems to indicate that this species is not closely related to other known *Ceromya s.s.* species. *C. lutea* is interpreted as a member of *Ceromya s.s.* because it has tiny spinules on the anterior (membranous) portion of the pregonite.

Setulation of wing vein R_{4+5} is a markedly labile character within siphonine lineages (Table 1), though all *Ceromya s.l.* species except *C. cephalotes, C. natalensis* and *C. monstrosicornis* have R_{4+5} setulose beyond *r-m.* The placement of these three species in *Ceromya* was carefully evaluated because the monophyly of *Ceromya s.l.* is not well established, and *Entomophaga* and *Proceromyia* species are also characterized by R_{4+5} not setulose beyond *r-m.* The male genitalia of *C. cephalotes* and *C. natalensis* were examined, and though spinules are absent from the pregonite, other features of the male genitalia indicate that the former belongs to the *C. bicolor* group and the latter is closely related to *C. languidula.* Both species

are therefore retained in *Ceromya s.s.* The placement of *C. monstrosicornis* in *Ceromya s.s.* is more equivocal because the male genitalia were unavailable for study and for other reasons discussed below.

Stein described *C. monstrosicornis* in 1924 in a new monobasic genus, *Stenoparia*. Mesnil (1963a) classified *Stenoparia* as a subgenus of *Ceromya*, adding *C. nigrohalterata* to the taxon. Species of *C. (Stenoparia)* and *C. (Proceromyia)* were separated from those of *Ceromya s.s.* by not having wing vein R_{4+5} setulose beyond crossvein *r-m*, and the latter (with single species *C. macronychia*) was separated from the former by its larger tarsal claws and several other minor differences (1963a: 829). In the classification adopted here, *C. macronychia* and *Nipponoceromyia pubioculata* (described after Mesnil's Palearctic revision) are included in the genus *Proceromyia*, and *C. nigrohalterata* is included in the genus *Entomophaga* with *E. exoleta* (see Phylogenetics sections of *Proceromyia* and *Entomophaga*).

There is insufficient evidence to place *C. monstrosicornis* in *Entomophaga* or *Proceromyia* (it certainly is not a *Goniocera* species). This species lacks the elongate aristomere 1 of *Entomophaga* or large tarsal claws of *Proceromyia*, and does not have a long preapical *ad* seta on the fore tibia which is common to both. Yet *C. monstrosicornis* is the only *Ceromya s.l.* species with a bare prosternum (as in *Proceromyia*), one of only three *Ceromya s.l.* species with R_{4+5} not setulose beyond *r-m*, and has a dark, uniformly pruinose abdomen as in *Entomophaga* and *Proceromyia*. Unfortunately, a male specimen of *C. monstrosicornis* could not be located in North American or European collections (and the male type could not be located in the ZMHU), so the phylogenetically important characters of the male genitalia could not be studied. *C. monstrosicornis* is left in *Ceromya s.s.* (not in *Ceromya s.l.*, as it is certainly not a member of the *C. silacea* sp. grp.) until its male genitalia are studied and its relationship to *Ceromya*, *Entomophaga* and *Proceromyia* established.

The placement of two undescribed species, Australia sp. 3 and Nepal sp. 1, in *Ceromya s.s.* also requires explanation. These species differ from other *Ceromya s.l.* species in having a long preapical *ad* seta on the fore tibia. They share this state with *Entomophaga* and *Proceromyia* species and some species of *Goniocera* and *Actia*, so the phylogenetic interpretation of this state in these *Ceromya* species is relevant to their placement. These species are certainly not close to *Actia*, so the discussion which follows focuses on their possible affinities with the other three genera.

Australia sp. 3 is known only from adult females and first instars, so pertinent characters of the male genitalia are unknown. Females of this species are unusual among *Ceromya* species in having enlarged tarsomere 5 on all legs and a sharply keeled sternum 7, while the first instar has an uncharacteristically broad labrum. These states are evidently autapotypies as they are not shared with the non-*Ceromya* genera mentioned above. External characteristics of the female favour the placement of Australia sp. 3 in *Ceromya s.s.*, though it is noted that examination of the male

genitalia would provide valuable information about this species' affinities.

The placement of Nepal sp. 1 is enigmatic, as it appears to belong in *Goniocera, Entomophaga, Proceromyia* or *Ceromya*, but lacks the synapotypies of any of these. Its placement is complicated further by its unusual combination of character states: (1) haired parafacial (with several larger setulae) in common with all but one *Goniocera* species (though the parafacial is more heavily setulose in those species than in Nepal sp. 1; Fig. 1), *Proceromyia pubioculata* and *Ceromya monstrosicornis* (both with hairs only on parafacial; Fig. 3), (2) long preapical *ad* seta on fore tibia (as mentioned above), (3) haired prosternum (shared with most siphonines, but not *Proceromyia* and some *Goniocera* species), (4) R_{4+5} setulose beyond *r-m* (as in *Goniocera* species and almost all *Ceromya* species, but not *Entomophaga* and *Proceromyia* species), and (5) uniformly pruinose abdomen (as in *Goniocera, Proceromyia* and *Entomophaga* species, and *C. monstrosicornis* but not other *Ceromya* species). I have been unable to polarize these states with confidence, so cannot interpret their phylogenetic significance (see also Evolution chapter under Phylogenetics of non-*Siphona s.l.* siphonine lineages). The male genitalia of Nepal sp. 1 do not closely resemble those of the aforementioned non-*Ceromya* genera, but similarly lack the typical spinules on the pregonite possessed by most *Ceromya s.s.* species (male genitalia of *C. monstrosicornis* unavailable for study) and has an aedeagus which cannot be placed into a *Ceromya s.s.* species group (though very different from the typical shape in the *Ceromya silacea* species group).

Such an array of character states in Nepal sp. 1 is not easily interpretable, and any placement at this time is tentative at best. This species seems to share more states with species of *Ceromya s.s.* (see description of *Ceromya s.s.*, which includes Nepal sp. 1) than with species of the other genera discussed, so is placed here for the present. A possible relationship with *C. monstrosicornis* needs to be investigated.

Geographic distribution

Thirty-nine described species are assigned to *Ceromya s.s.*, of which only eight are New World in distribution (see Sabrosky and Arnaud 1965 for ranges of species north of Mexico, Guimarães 1971, Cortés 1967, and Cortés and Hichins 1969 for ranges of species south of the United States). However, preliminary study of specimens of New World *Ceromya s.s.* indicates that the number of described species is a significant underestimate of the true diversity of the group in the New World. I estimate from examined material that there are about 15 undescribed New World species, almost all Neotropical in distribution.

Most accurately known are the British (Crosskey 1976b) and European (Draber-Mońko 1981, Herting 1984) faunas, consisting of five described species. A key for recognition of all of these species has not been published, though they are treated in part in Mesnil (1963a) and Herting (1977). The fauna of Asia is less well documented, and appears to be depauperate. *C. bicolor* is the only *Ceromya s.s.* species recorded from central Asia (Richter 1971, 1975, 1980), and the only other

described eastern Palearctic species, *C. pruinosa*, is apparently restricted to Japan (though Herting 1984 cites this species as a possible synonym of *C. bicolor*). However, I have seen specimens of several undescribed species of *Ceromya s.s.* collected from Nepal.

Greatest diversity of described *Ceromya s.s.* species in the Old World is recorded from the tropics: eight species in the Afrotropical region and 13 in the Oriental region (distributions given in Crosskey 1980, 1976a, respectively; key to Philippine species in Dear and Crosskey 1982, though these authors include *S. (Aphantorhaphopsis)* in their concept of *Ceromya*). Only three species are described from Australia (Crosskey 1973). Still, the described portion of the Old World fauna of *Ceromya s.s.* belies its true diversity: Shima (pers. comm.) has tentatively recognized close to 20 new species in the Oriental region, and I have seen specimens of numerous undescribed species from Australia and Africa.

From a cosmopolitan perspective *Ceromya s.s.* can best be considered a tropical group, with relatively few species in the Nearctic and Palearctic regions. The genus still requires a great deal of descriptive work, especially with respect to its tropical elements.

List of described species included in *Ceromya sensu stricto*

S   *amblycera* (Aldrich), 1934: 132 (*Actia*). Holotype male, Argentina: Bariloche (USNM). Holotype examined. **New combination**, moved from *Actia*.

N   *americana* (Townsend), 1892: 69 (*Thryptocera*). Holotype male (not female), USA: D.C., Washington (UKL). Holotype examined.

    syn.   *elyii* (Walton), 1914: 91 (*Polychaetoneura*). Three female syntypes, USA: Connecticut, East River (USNM).— Curran, 1933a: 5. Syntypes examined.

A   *amicula* Mesnil, 1954: 40. Holotype male, Zaire: Bambesa (MRAC). Holotype examined.

O   *apicipunctata* (Malloch), 1926: 510 (*Actia*). Holotype male, Philippines: Luzon, Benquet (USNM). Holotype examined.

O   *bellina* Mesnil, 1957: 44. Holotype male, Burma: Kambaiti (ZMU). Holotype examined.

P   *bicolor* (Meigen), 1824: 354 (*Tachina*). Holotype male, no locality data (MNHN).

    syn.   *testacea* Robineau-Desvoidy, 1830: 88. Type(s), France: Lille (lost).— Herting, 1974: 18.

            rufina (Zetterstedt), 1838: 641 (*Tachina*). Holotype female, Sweden: Dalecarlia (UZI).— Herting, 1984: 121.

            fasciata (Stein), 1924: 132 (*Actia*). Lectotype female (by designation of Herting, 1977: 10), Yugoslavia: Sarajevo (NMBA).— Considered a possible color variant of *bicolor* Mg. by Herting, 1977: 10.

A *buccalis* (Curran), 1933c: 163 (*Actia*). Holotype male, Zimbabwe: Gatooma (AMNH). Holotype examined.

O *capitata* Mesnil, 1957: 42. Holotype male, Burma: Kambaiti (ZMU). Holotype examined.

O *cephalotes* Mesnil, 1957: 40. Holotype male, Burma: Kambaiti (ZMU). Holotype examined.

A *cibdela* (Villeneuve), 1913: 35 (*Actia*). Lectotype male (**by designation in text**), Nigeria: Oshogbo (CNC). Lectotype examined.

    syn.   *cibdella*. Incorrect subsequent spelling of *cibdela* Villeneuve (Curran, 1927a: 323).

S *cornuta* (Aldrich), 1934: 131 (*Actia*). Holotype male, Chile: Angol (USNM). Holotype examined. **New combination**, moved from *Actia*.

P *dilecta* Herting, 1977: 10. Holotype male, Switzerland: Gordola (SMNS). Holotype examined.

O *dubia* (Malloch), 1930b: 146 (*Actia*). Holotype female, Malaysia: Selangor (BMNH). Holotype examined.

A *femorata* Mesnil, 1954: 38. Holotype male, Zaire: Bambesa (MRAC). Holotype examined.

U *fergusoni* (Bezzi), 1923b: 657 (*Schizotachina*). Holotype male, Australia: New South Wales, Sydney (type missing according to Crosskey, 1973: 137).

    syn.   *fergussoni*. Incorrect subsequent spelling of *fergusoni* Bezzi (Curran, 1927b: 355-356).

P *flaviceps* (Ratzeburg), 1844: 172 (*Musca* (*Tachina*)). Type, Germany (lost).

    syn.   *flaviceps* (Stein), 1924: 134 (*Actia*).— Objective synonym; see Herting, 1982: 8 and 1984: 190 (note 94), *cf.* Herting, 1977: 9.

P *flaviseta* (Villeneuve), 1921: 45 (*Actia*). Male syntype from Berlin, Germany, female syntype from Samara, USSR (CNC). Syntypes examined.

O *hirticeps* (Malloch), 1930b: 146 (*Actia* (*Pseudactia*)). Holotype male, Malaysia: Kedah Peak (BMNH). Holotype examined.

U *invalida* (Malloch), 1930a: 305 (*Actia* (*Schizoceromyia*)). Holotype male, Australia: New South Wales, Sydney (SPHTM). Holotype examined.

A *languidula* (Villeneuve), 1913: 36 (*Actia*). Two male syntypes, Nigeria: Oshogbo (BMNH and CNC). Syntypes examined.

A *languidulina* Mesnil, 1977b: 178. Holotype female, Madagascar: Ambohitantely (MNHN).

O *latipalpis* (Malloch), 1930b: 145 (*Actia*). Holotype female, Malaysia: Kedah Peak (BMNH). Holotype examined.

A *lavinia* (Curran), 1927a: 324 (*Actia*). Holotype female, South Africa: Natal, Clan Syndicate (PPRI). Holotype examined.

O *longimana* Mesnil, 1957: 38. Holotype female, Burma: Kambaiti (ZMU). Holotype examined.

S *lutea* (Townsend), 1927: 283 (*Actinactia*). Holotype male, Brazil: São Paulo

(USNM). Holotype examined. **New combination**.

A   *luteicornis* (Curran), 1933c: 162 (*Actia*). Holotype male, southern Zimbabwe (BMNH). Holotype examined.

O   *maculipennis* (Malloch), 1930b: 141 (*Actia*). Holotype male, Malaysia: Selangor (BMNH). Holotype examined.

P   *monstrosicornis* (Stein), 1924: 128 (*Stenoparia*). Holotype male, German Democratic Republic: Mecklenburg (ZMHU; not located, possibly lost).

    syn.   *monstruosicornis*. Incorrect subsequent spelling of *monstrosicornis* Stein (Mesnil, 1963a: 829, 831).

A   *natalensis* (Curran), 1927a: 325 (*Actia*). Holotype male, South Africa: Natal, Cramond (PPRI). Holotype examined.

N   *ontario* (Curran), 1933a: 4 (*Actia*). Holotype female, Canada: Ontario, Lake of Bays, Norway Point (CNC). Holotype examined.

N   *palloris* (Coquillett), 1895b: 50 (*Lasioneura*). Lectotype male (by designation of Coquillett, 1897: 58), USA: New Hampshire (USNM). Lectotype examined.

O   *portentosa* Mesnil, 1957: 43. Holotype female, Burma: Kambaiti (ZMU). Holotype examined.

P   *pruinosa* Shima, 1970c: 188. Holotype male, Japan: Hokkaido, Berabonai (BLKU). Paratype examined.

O   *punctipennis* (Malloch), 1930b: 140 (*Actia*). Holotype male, Malaysia: Kedah Peak (BMNH). Holotype examined.

O   *punctum* (Mesnil), 1953: 107 (*Actia*). Holotype male, China: Canton (BMNH). Holotype examined.

O   *rotundicornis* (Malloch), 1930b: 145 (*Actia*). Holotype male, Malaysia: Pahang, Fraser's Hill (BMNH). Holotype examined.

S   *subopaca* (Aldrich), 1934: 133 (*Actia*). Holotype male, Argentina: Bariloche (BMNH). Holotype examined.

S   *unicolor* (Aldrich), 1934: 133 (*Actia*). Holotype male, Argentina: Bariloche (BMNH). Holotype examined.

U   *valida* (Curran), 1927b: 356 (*Actia* (*Schizactiana*)). Holotype male, Australia: Queensland, Palmerston (DEI). Holotype examined.

Nomen dubium

P   *erythrocera* Robineau-Desvoidy, 1830: 87. Type(s), France (lost).

List of examined, undescribed, species included in *Ceromya sensu stricto*

Ceromya nr. *punctipennis*: Two males from se. Popondetta, New Guinea (BLKU).

Ceromya Australia sp. 1: Two males from Queensland (CNC, DPI).

Ceromya Australia sp. 2: Three males, one female from Queensland (DPI).

Ceromya Australia sp. 3: One female from Mt. Glorious, Queensland (DPI).

Ceromya Australia sp. 5: One male, two females from Mt. Glorious, Queensland (DPI).

Ceromya Brazil sp. 1: Males and females from Nova Teutonia (CNC, USP).
Ceromya Brazil sp. 3: One male from Amazonas (INPA).
Ceromya Brazil sp. 4: One male from Nova Teutonia (CNC).
Ceromya Chile sp. 1: One male and one female from Magellanes (CNC).
Ceromya Chile sp. 2: One male from Isla de Chiloé (CNC).
Ceromya Mexico sp. 1: Three males and two females from Durango (CNC).
Ceromya Mexico sp. 2: One male each from Colima (UCB) and Chiapas (CNC).
Ceromya Mexico sp. 3: One male from Chiapas, one female from Veracruz (CNC). Two possibly conspecific males from SE Brazil (CNC).
Ceromya Mexico sp. 4: One male from Chiapas (CNC).
Ceromya Mexico sp. 5: One male from Veracruz (CNC). One male and several females possibly conspecific from SE Brazil (CNC, USP).
Ceromya Nepal sp. 1: Males and females from Nepal (CNC).
Ceromya Nepal sp. 3: Two males, one female from 28°00'N 85°00'E (CNC).
Ceromya Nepal sp. 4: One female from 28°00'N 85°00'E (CNC).
Ceromya Nepal sp. 5: One male, one female from Kathmandu (CNC).
Ceromya New Guinea sp. 4: Two males from se. Popondetta (BLKU).
Ceromya New Guinea sp. 5: One male each from se. Popondetta and Nabire (BLKU).
Ceromya New Guinea sp. 6: Two males from Wau (BLKU).
Ceromya New Guinea sp. 11: Two males from Mt. Kaindi (BLKU).
Ceromya New Guinea sp. 15: One male from Mt. Kaindi (BLKU).
Ceromya New Guinea sp. 18: One male each from Mt. Kaindi and se. Mt. Giluwe (BLKU).
Ceromya Peru sp. 1: One male from Quincemil, Cuzco (CNC).
Ceromya U.S. sp. 1: One male from Adair Co., Missouri (MSU)

<div align="center">

Ceromya silacea (Meigen) species group
Figs. 35, 37, 52, 84, 112, 148, 159.

</div>

Recognition

Male genitalic features provide the only characteristics by which members of the *Ceromya silacea* species group (a strictly Old World taxon) can be distinguished from *Ceromya s.s.* species. Species of *C. silacea* species group are unique within the Siphonini in possessing posteriorly on the distiphallus an infolded and sclerotized structure (Fig. 112) - in other siphonines the posterior margin is sclerotized or membranous (the latter in all but a very few species), but not infolded.

Ceromya silacea is one of the species with greatest development of the infolded structure on the distiphallus. As shown in Fig. 112, this structure is extended anteriorly to near the anterior margin of the distiphallus (note too that the distiphallus is extensively membranous anteriorly and laterally in this species) and projects posteriorly from between the posterolateral margins. In some other species of this species group the infolded structure is smaller.

The pregonite of species of the *C. silacea* species group is long and sickle-like in most species (Fig. 84) and shorter and apically rounded in others; the membranous portion is not expanded and spinules are absent (*cf. Ceromya s.s.* section and Figs. 39-40, 77-83).

Description

Length: 3.0-5.5mm.

Head.— Five frontal setae in most species, three (*C. silacea*) or four in a very few; normal arrangement. Anterior proclinate orbital seta longer than posterior one. Eye size of male medium-large to large, 0.77-0.86 head height; size in female subequal to that of male. Flagellomere 1 of male medium-short to medium length, 0.47-0.56 head height; shape from linear to large and almost triangular, not bifid. Flagellomere 1 of female smaller than in male. Aristomere 1 short. Aristomere two 1.5-5X longer than wide. Aristomere 3 rather short to long and evenly tapered; micropubescent to pubescent. Clypeus U-shaped. Palpus short, clavate. Proboscis with prementum short, labella padlike.

Thorax (Figs. 35, 37).— Prosternum setulose. Lower proepimeral seta weak, not directed downward. Katepisternum bare anterior to mid coxa. Lower katepisternal seta much shorter than upper anterior seta in most species, subequal in length to it in three closely related species: *C. normula*, *C. similata* and *C. varichaeta*. Three or four postsutural dorsocentral setae. Upper part of anepisternum with single setula. Fore tibia with preapical *ad* seta much shorter than *d* seta. Mid tibia with one *ad* seta. Mid femur with pilose patch on anterior surface from about midlength to distal end in males of *C. normula* and *C. varichaeta* (Fig. 35). Tarsomeres normal in size, claws small. Wing: CuA_1 with distal portion 0.29-0.47X length of proximal portion (mean 0.36); anal vein not extended to wing margin. Wing setulae: R_1 dorsally bare, or distally or entirely setulose, ventrally bare or distally setulose; R_{4+5} setulose from base to beyond *r-m*; CuA_1 bare or setulose.

Abdominal terga 1-5.— Abdomen ovoid in shape. T_{1+2} without median marginal setae; lateral marginal setae absent to strong. T_3-T_5 average or with weak lateral discal setae.

Male genitalia (Figs. 52, 84, 112).— S_5 with, inner (or posterior) margins of processes obtusely angled to almost transverse (Fig. 52 and Shima 1970c, figs. 3d,e); apical lobe undifferentiated to rounded; median lobe rounded or pointed in most species, slightly flattened medially in *C. varichaeta* (but not to degree found in *Goniocera*); without accessory lobe; processes very sparsely setulose (most species) to densely setulose (*C. varichaeta*). T_6 present as pair of small lateral sclerites. Ejaculatory apodeme with fan-shaped portion half to subequal width of hypandrial apodeme. Pregonite in profile long and sickle-like in most species (Fig. 84), apically rounded in *C. varichaeta*; bare. Epiphallus absent from most species, present in *C. varichaeta*. Distiphallus (Fig. 112) broad in profile, with short to long posterolateral arm except in *C. varichaeta*, and unique infolded and sclerotized structure formed from posterior surface (large in most species, very small in *C. varichaeta*) which is deeply U-shaped in posterior view. Postgonite large, apically bilobed. Surstylus average length to long, straight in a few species (*e.g.* Shima 1970c, fig. 5b), thin and curved posteriorly in most (*e.g., op. cit.*, fig. 5a); with long hairs along length in *C. varichaeta* (also found in *C. languidula* of *Ceromya s.s.*); basally fused with epandrium or free (*C. varichaeta*). Cerci rather short to average length, posteriorly deeply inflexed at midlength (*e.g., op. cit.*, fig. 5b) to gently curved or almost straight (*e.g., op. cit.*, fig. 5a); moderately to densely setose on basal half.

Examined male genitalia of: *C. mellini*, *C. silacea*, *C. varichaeta*, Australia sp. 4 and Nepal sp. 2. Examined published figures of: *C. dorsigera* and *C. silacea* (both in Shima 1970c, figs. 3d,e, 5).

Female genitalia (Fig. 148).— (Only *C. silacea* examined.) Medium length (slightly extensible). S_6 with average length hairs. T_6 present as two lateral sclerites; enclosing spiracles of segment 6 in anteroventral portion. S_7 with anterior apodeme; without posteromedial keel. T_7 present as two lateral sclerites; spiracles of segment 7 enclosed within anterior portion of T_7. S_8 distinctly developed, haired. T_{10} present as two distinct sclerites.

Examined female genitalia of: *C. silacea*.

Taxonomic changes

Status of Ceromya similata Mesnil.— Mesnil described *Ceromya similata* in 1954 as a sympatric subspecies of *C. varichaeta* (Curran), noting that it differs from the nominal subspecies primarily in having R_1 distally rather than entirely setulose dorsally. As explained elsewhere (*e.g.* Taxonomic changes section of *Siphona (Siphona)*), I do not accept the concept of sympatric subspecies; therefore, *C. varichaeta similata* must either be elevated to species status or declared conspecific with *C. varichaeta*.

I have examined the holotypes of *C. varichaeta* and *C. similata*, and a closely related species *C. normula* (the latter placed in *Peribaea* by Crosskey, 1980). *C. varichaeta* and *C. normula* are based on males which share a striking synapotypy: a pilose patch anteriorly on the mid femur (Fig. 35). The types differ little except that R_1 is dorsally setulose entirely in *C. varichaeta* and only distally in *C. normula*. This difference in R_1 setulation is very reliable as a species specific character (in contrast to the states R_1 distally bare or setulose), so I accept *C. varichaeta* and *C. normula* as valid species. Setulation of R_1 in the holotype of *C. similata* matches that of *C. normula*, not *C. varichaeta*, and might be conspecific with that species. However, the type of *C. similata* is female (thus lacking the male-linked pilose patch on mid femur), so is difficult to compare critically with the male types of the other two nominal species. Though *C. similata* has been associated with *C. varichaeta* in publications, it is more likely conspecific with *C. normula* or a valid species. I treat *C. similata* here as a valid species pending examination of additional male and female specimens of the three nominal species.

Hosts

Hosts have only been recorded for two species, and both belong to the Noctuidae (Table 2).

Phylogenetics

Adults of the *C. silacea* species group are similar to those of *Ceromya s.s.* externally, but differ in two important male genitalic characteristics. First, they lack spinules on the membranous anterior portion of the pregonite, which are present in most *Ceromya s.s.* species and are interpreted as synapotypic of that group. Second, they have a uniquely infolded posterior margin on the distiphallus (Fig. 112), which is interpreted as synapotypic of the *C. silacea* species group (monophyly of *Ceromya s.l.* discussed in Evolution chapter).

In *C. silacea, C. mellini,* Australia sp. 4 and Nepal sp. 2, the infolded region of the distiphallus is very large (Fig. 112). In *C. varichaeta* the infolded region is small and nearer the apex, and perhaps represents a more primitive condition. The male genitalia of the other species placed in this group were not examined, but these species are thought to belong here because they appear very similar externally to certain well established members of this group. These species should be removed from the *C. silacea* group if they are found to lack the synapotypy (of the distiphallus) of this group.

The labrum is hook-like in the first instar of *C. silacea* (Fig. 159) and hatchet-like or intermediate in other examined *Ceromya s.l.* species (see O'Hara in press "a"). It remains to be determined whether this feature is another synapotypy of the *C. silacea* species group.

Geographic distribution

The eight described species of the *Ceromya silacea* species group are exclusively Old World in distribution. The centre of diversity is the Old World tropics (see Crosskey 1976a and 1980 for ranges of Oriental and Afrotropical species; none described from Australia), with only three species recorded from the Palearctic region: *C. dorsigera* (described from Switzerland and recorded from Japan by Shima 1970c), *C. silacea* (widespread, with records from England (Crosskey 1976b), Eurasia (Mesnil 1963a, Shima 1970c, Richter 1971, 1976b, 1980, Draber-Mońko 1981), and southern India (examined specimens from CNC)), and *C. pendleburyi* (SE Asia and Japan, Mesnil 1963a and Shima 1970c). The three Palearctic species are keyed in Shima (1970c). In addition to the described species I have seen specimens of a new species from Nepal (Nepal sp. 2) and another from Australia (Australia sp. 4) [numbers used here for new species refer to *Ceromya s.l.*].

List of described species included in the *Ceromya silacea* species group

P   *dorsigera* Herting, 1967a: 8. Holotype male, Switzerland: Gordola (SMNS). Holotype examined.

O   *mellina* (Mesnil), 1953: 109 (*Actia*). Holotype male, Burma: Kambaiti (ZMU). Holotype examined.

A   *normula* (Curran), 1927a: 322 (*Actia*). Holotype male, South Africa: East London (PPRI). Holotype examined. **New combination**, moved from *Actia*.

O   *patellicornis* Mesnil, 1957: 40. Holotype male, India: Darjeeling (BMNH). Holotype examined.

O,P *pendleburyi* (Malloch) 1930b: 144 (*Actia*). Holotype male, Malaysia: Pahang (BMNH). Holotype examined.

O,P *silacea* (Meigen), 1824: 355 (*Tachina*). Holotype male, no locality data (MNHN).
      syn.   *siebeckii* (Sintenis), 1897: 151 (*Thryptocera*). Holotype female, Estonia: Pärnu (not located).— Herting, 1984: 121.

A   *similata* Mesnil, 1954: 39 (as subspecies of *Ceromya varichaeta* (Curran)). Holotype female, Zaire: Tshumba (MRAC). Holotype examined. **New status.**

A   *varichaeta* (Curran), 1927c: 6 (*Actia*). Holotype male, Zaire: Faradje (AMNH). Holotype examined.

List of examined, undescribed, species included in the *Ceromya silacea* species group

Ceromya Australia sp. 4: One male, one female from Queensland (DPI).
Ceromya Nepal sp. 2: Males from 28°00'N 85°00'E (CNC).

Genus *Actia* Robineau-Desvoidy

Figs. 8-10, 21, 23, 29, 31, 33, 41-42, 58-59, 85-86, 117-119, 151-152, 160.

Actia Robineau-Desvoidy, 1830: 85. Type-species, *Roeselia lamia* Meigen, 1838, by designation of I.C.Z.N., 1987: 71 (Opinion 1432).

Thryptocera Macquart, 1834: 310. Type-species, *T. bicolor* Macquart, by designation of Townsend, 1916: 624) = *Tachina crassicornis* Meigen, 1824.— Herting, 1976: 3.

Tryptocera. Variant spelling of *Thryptocera*.

Gymnophthalma 1838, Lioy, 1864: 1341. Type-species, *Tachina crassicornis* Meigen, 1824 (monotypy).

Gymnopareia Brauer and Bergenstamm, 1889: 103 (35). Type-species, *Tachina crassicornis* Meigen, 1824 (monotypy).

Gymnoparia. Variant spelling of *Gymnopareia*.

Actiopsis Townsend, 1917: 121. Type-species, *A. autumnalis* Townsend, 1917 (original designation).

Setasiphona Townsend, 1934: 248. Type-species, *Actia siphonosoma* Malloch, 1930 (original designation).

Recognition

Actia is a diverse genus of cosmopolitan distribution. With few exceptions, members are recognized externally by the presence of a row of hairs on the katepisternum anterior to the mid coxa (*cf.* Figs. 33 and 34). Among other siphonines, only the European species *Entomophaga exoleta* shares this state, and is distinguished from *Actia* by its elongate aristomere 1 (Fig. 4), long preapical *ad* seta on fore tibia, and features of the male genitalia (especially sternum 5 - *cf.* Figs. 50 and 58-59). Five *Actia* species, *A. completa* and *A. magnicornis* from Malaysia and *A. parviseta*, *A.* nr. *parviseta* and Australia sp. 5 from eastern Australia, either lack this row of katepisternal hairs or the number of hairs is reduced. These species have two setulae on the upper portion of the anepisternum (see below), and males are additionally recognized as members of *Actia* by their V-shaped sternum 5 (similar to Figs. 58-59) and spined pregonite (similar to Figs. 85-86).

The upper portion of the anepisternum has two setulae in almost all *Actia* species (Fig. 31; one setula in most other siphonines, Fig. 32). Two setulae are present in a few *Peribaea* species and a few species in different *Siphona s.l.* lineages, but this state seems to be restricted to *Actia* among siphonines in which the anal vein does not extend to the wing margin (Table 1).

Three *Actia* species, *A. completa* and *A. fulvicauda* from Malaysia and *A. chrysocera* from the Seychelles Islands, are the only known siphonines other than *Peribaea* and *Siphona s.l.* species to have the anal vein extended to the wing margin. *A. fulvicauda* and *A. chrysocera* possess a row of katepisternal hairs as in most other *Actia* species, but *A. completa* has an incomplete row. *A. completa* is recognized as an *Actia* species by its V-shaped sternum 5, spined pregonite and two anepisternal setae (as mentioned above).

Males of most *Actia* species have a more or less V-shaped sternum 5, with little or no constriction of the median lobes above the median cleft (Figs. 58-59). Sternum 5 departs slightly from this shape in a few species, but even in these it more closely resembles the sternum 5 of other *Actia* species than non-congeneric siphonines.

The only feature apparently universal among (and unique to) *Actia* species is a J-shaped, spinose pregonite (Figs. 41-42 and 85-86). All examined male genitalia of *Actia* species were of this type, including species mentioned above as having atypical external features.

Description

Length: 2.5-6.0mm.

Head (Figs. 8-10).— Five frontal setae (rarely four), normal arrangement. Anterior proclinate orbital seta longer than posterior one in almost all species. Eye of male small to large, 0.65-0.89 head height; eye of female subequal to or slightly smaller than in male. Flagellomere 1 of male markedly varied in length, 0.43-0.75 head height; linear to broad; bifid in only one known species, *A. yasumatsui* (Shima 1970b, fig. 1). Flagellomere 1 of female smaller than in male or subequal in size; not bifid. Aristomere 1 short. Aristomere 2 varied from 1.5-5X longer than wide, relatively short (2-3X) in most species. Aristomere 3 short and thickened to near tip, to long and evenly tapered; almost bare to short plumose. Clypeus varied from narrow and enclosed in membrane to broadened or U-shaped. Palpus short in most species, long in some species with elongate proboscis; enlarged apically in females of a few species; clavate. Prementum short to long, in a few Old World species of latter slender and elongate like typical *Siphona* species (Fig. 9). Labella also markedly varied, padlike or slightly lengthened (like in *Siphonopsis*) in most species, quite elongate (half head height or longer) and with numerous pseudotracheae and flexible in life in a few species (*e.g. A. fallax, A. jocularis, A. longilingua*); in a very few Old World species labella as in *Siphona* species (Fig. 9): about head height in length, basal portion inflexible in life, with reduced number of pseudotracheae apically (*e.g. A. malaisei*).

Thorax (Figs. 21, 23, 29, 31, 33).— Prosternum setulose in almost all species (apparently bare only in *A. nigra*). Lower proepimeral seta weak or absent. Most species with row of hairs on katepisternum directly anterior to mid coxa extended upward almost to lower katepisternal seta (Fig. 33); several hairs in lower corner only (*i.e.* groundplan condition of Siphonini) in *A. parviseta* and *A.* nr. *parviseta*, and several hairs in lower corner to row extended halfway to lower katepisternal in *A. completa, A. magnicornis* and Australia sp. 5. Lower katepisternal seta shorter (in most species much shorter) than upper anterior seta (Fig. 31). Four postsutural dorsocentral setae in most species, three in a few. Upper part of anepisternum with two setulae in most species (Fig. 31), with single setula in a very few. Fore tibia with preapical *ad* seta much shorter than *d* seta in most species, ranging to about 0.75 length of *d* seta in a few species (known in *A. infantula, A. lamia* and *A. nudibasis*), and subequal to *d* seta in a few species (known in *A. eucosmae, A. nigriventris, A. parviseta*, and several undescribed Australian species). Mid tibia with one *ad* seta in almost all species (markedly reduced or absent from *A. eucosmae, A. parviseta, A. perdita* and Australia sp. 3). Tarsomeres normal in size, or tarsomere 5 of fore leg broadened (known only in female of *A. tarsata*, though slightly larger than average in females of a few other species), tarsomere 5 of all legs slightly enlarged in female of *A. nigriventris*; claws short. Wing (Fig. 21) with vein *M* complete in most species, slightly developed or absent after bend in some (*e.g. A eucosmae, A. exsecta, A. lamia, A. munroi, A. nigriventris, A. perdita, A. pulex, A. rufescens* and *A. takanoi*); vein CuA_1 with distal portion 0.25-1.6X length of proximal portion (in most species short, 0.3-0.7; mean 0.56); anal vein not extended to wing margin, except in *A. completa, A. fulvicauda* and faintly in *A. chysocera*. Wing setulae: R_1 dorsally bare, or distally or entirely setulose, ventrally bare or distally setulose; R_{4+5} setulose from base to or beyond *r-m*; CuA_1 bare or setulose; unusual patterns in a few species with additional veins setulose: *A. ciligera* (R_{2+3}, R_{4+5} and *M* setulose dorsally and ventrally) *A. fallax* (*M* setulose ventrally) and *A. gratiosa* (*Sc* setulose dorsally).

Abdominal terga 1-5.— Abdomen ovoid in shape in most species, slightly elongate in a very few. T_{1+2} without median marginal setae; lateral marginal setae absent from most species, strong in a few. T_3-T_5 average in most species, with weak lateral discal setae in a few (particularly among species in Holarctic region).

Male genitalia (Figs. 41-42, 58-59, 85-86, 117-119).— S_5 little varied, processes elongate, rounded or pointed posteriorly, inner margins approximately V-shaped in most species (Fig. 58), obtusely angled in a very few (Fig. 59; rarely as much as in other siphonines); median lobe undifferentiated (Fig. 58) or scarcely differentiated (Fig. 59); median cleft scarcely constricted posteriorly by median lobes in most species (Fig. 58), distinctly constricted by rounded (Fig. 59) to elongate median lobes in a few; processes moderately setulose with several pair of large setae. T_6 slightly sclerotized, generally continuous dorsally. Ejaculatory

apodeme varied from small to very large (0.5-2.0X width of hypandrial apodeme), in most species width of fan-shaped portion subequal to width of hypandrial apodeme. Pregonite (Figs. 85-86) broad subapically and approximately J-shaped, outer surface short spinose on apical half or less; asetose. Epiphallus absent. Distiphallus (Figs. 117-119) with posterior margin partially developed in some species, absent from others; not laterally broadened as in *Peribaea* species; in profile from broad and truncate apically to very narrow and sharply pointed apically (Fig. 119), with numerous forms between. Postgonite in most species apically broad, rounded or truncate, in a few species narrow or intermediate in width. Surstylus short to long, shape varied relatively little, narrow or broad in a few species, intermediate in most; medium to long hairs basally in some species of an Old World group; basally free from epandrium. Cerci varied little, short to average length, sharply inflexed at midlength in some species, smoothly curved posteriorly in most; moderately setose on basal half.

Examined male genitalia of: *A. autumnalis, A. brevis, A. completa, A. diffidens, A. infantula, A. interrupta, A. lamia, A. longilingua, A. magnicornis, A. malaisei, A. nitidella, A. nudibasis, A. parviseta, A. pilipennis, A. rufescens,* Australia spp. 1-2,4-5, Jamaica sp. 1, Liberia sp. 1, Mexico sp. 1, Nepal spp. 1-2, New World spp. 1-19 and Uganda sp. 1. Examined published figures of: *A. lamia* (Andersen 1983, fig. 25), *A. darwini, A. painei* (both in Crosskey 1962, figs. 1-6), *A. jocularis, A. nigra* (both in Shima 1970c, figs. 2, 3b,c, 4), *A. pokharana* and *A. yasumatsui* (both in Shima 1970b, fig. 2).

Female genitalia (Figs. 151-152).— Short and markedly uniform and unspecialized, with only minor differences among species. S_6 with average length hairs. Spiracles of segment 6 enclosed in T_6; in some species T_6 forming a broad sclerite narrowly discontinuous dorsally, in others represented by two small lateral sclerites, in a few species unsclerotized. S_7 without anterior apodeme except for short projection in *A. crassicornis* (Andersen 1983, fig. 12); without posteromedial keel. T_7 absent or present only as two small lateral sclerites; spiracles of segment 7 in membrane between segments 6 and 7. S_8 distinctly developed, haired, with lateral edges curved inward. T_{10} distinctly developed as median sclerite, in most species subequal in size to S_8.

Examined female genitalia of: *A. diffidens, A. interrupta, A. lamia, A. malaisei, A.* nr. *parviseta,* Australia sp. 1, New World spp. 4-5 and Zaire sp. 1. Examined published figures of: *A. crassicornis* and *A. lamia* (both in Andersen 1983, figs. 11, 12).

Taxonomic changes

Synonymy of Actia brevis Malloch with Actia darwini Malloch.— The male holotypes of these nominal species were examined and compared. They differ primarily in abdominal coloration and setulation of vein CuA_1, but these characteristics vary within some species and the degree of difference present here is not unusual among conspecifics. I also examined other specimens from several localities in eastern Australia, and these exhibit states intermediate between those in the *A. brevis* and *A. darwini* types. I conclude that these types belong to the same species, and here synonymize *Actia brevis* Malloch (1930a) with *Actia darwini* Malloch (1929b).

Actia parviseta Malloch (Fig. 10).— Malloch described this species in 1930 and placed it in his widely defined *Actia.* Later Crosskey (1966: 109) shifted it to *Ceromya*, presumably because it lacks a row of hairs on the katepisternum anterior to the mid coxa - a characteristic usually diagnostic for *Actia*. Dissection of the male genitalia of the type revealed that they possess two *Actia* synapomorphies: a V-shaped S_5 and spinose pregonite. Furthermore, the female reproductive system of a specimen of a closely related species (*A.* nr. *parviseta*) was examined and contained first instars of the *Actia* type (*i.e.* dorsal cornu lacking from the cephalopharyngeal skeleton; Fig. 160 and O'Hara in press "a"). It thus appears that *Actia parviseta* and a few other species (*A. completa, A. magnicornis, A.* nr.

parviseta and Australia sp. 5) have a bare or sparsely haired katepisternum anterior to the mid coxa, while still possessing all other known synapomorphies of *Actia*.

Hosts

The hosts of *Actia* are better known than those of other siphonines, with records for about 20 *Actia* species (Table 2). Hosts belong predominantly to the Tortricidae, but a variety of other Microlepidoptera and a number of Macrolepidoptera are also parasitized. Host larvae vary in habit from small leaf miners and rollers to large, bare to hairy caterpillars which feed openly on vegetation. There is one record of an *Actia* species parasitic on a pyrrhocorid bug, *Dysdercus* sp. This record is doubtful, as Hemiptera are almost exclusively parasitized by phasiines among the Tachinidae.

Phylogenetics

A row of hairs on the katepisternum anterior to the mid coxa has long been considered a diagnostic feature of *Actia*. It is now apparent that several species belonging to the *Actia* lineage lack this row of hairs (see Recognition and Description sections). The relationships of these species to other *Actia* species is unknown, so the absence of a row of katepisternal hairs from these species cannot be positively polarized as primitive or derived. If derived, then these species must be descended from ancestors possessing a row of katepisternal hairs, and I consider this explanation the more reasonable at this time. This explanation is hypothesized because: 1) no other character states support the primitive position of these species within *Actia*, and 2) several of these species have a variable number of katepisternal hairs, ranging from a few to a nearly complete row; the varied extent of this row is more parsimoniously interpreted as a reversal from a complete to incomplete row rather than as an independent gain from an incomplete to complete row. Thus a row of hairs on the katepisternum is here considered a synapotypy of *Actia* species, with absence of this row in several *Actia* species interpreted as resulting from reversal(s) from the apotypic state.

Almost all *Actia* species have two setulae on the upper portion of the anepisternum (Fig. 31). Most other siphonines have one (Fig. 32), though two are present in a few species of *Peribaea* and a few species of most supraspecific taxa of *Siphona s.l.* (Table 1). This distribution suggests that two anepisternal setulae is the derived state within the tribe, though its many independent acquistions weaken its value as a synapotypy of *Actia*.

Several species of *Actia* have the anal vein extended to the wing margin (see Recognition and Description sections), but possess the derived genitalic states of *Actia*, and all but one of these (*A. completa*) have a katepisternal row of hairs. Extension of the anal vein to the wing margin probably arose independently in *Actia* and the *Peribaea-Siphona s.l.* lineage.

Sternum 5 is approximately V-shaped in most *Actia* species, and derivable from that shape in the others. The pregonite is J-shaped and spinose, and these states

appear to be universal among *Actia* species. It is hypothesized that these characteristics of the male sternum 5 and pregonite are synapotypies of *Actia* (the spinose pregonite proposed as an *Actia* synapotypy by Andersen 1983), and in combination are better diagnostic features of the genus than the row of katepisternal hairs discussed above and previously used to define the genus.

Another possible synapotypy of *Actia* species is lack of a dorsal cornu from the cephalopharyngeal skeleton of first instars (Fig. 160). First instars of all nine examined *Actia* species share this state, though the illustration of *Actia dubitata* by Farinets (1980) seems to indicate that a distinct dorsal cornu is present in that species (O'Hara in press "a"). Lack of a dorsal cornu is therefore either a synapotypy of *Actia* or a derived subgroup of *Actia*.

Previous placement of *Entomophaga exoleta* in *Actia* is discussed in the Phylogenetics section of *Entomophaga* Lioy.

Geographic distribution

Compared to 56 described species in the Old World, the *Actia* fauna of the New World (four described species in the Nearctic region and one in the Neotropical region) at first seems but a minor component of the world fauna. However, this paucity of described *Actia* species gives a false impression of the true diversity of this genus in the New World. I have examined specimens of several new Nearctic *Actia* species, and from relatively meagre collections of Neotropical *Actia*, have recognized close to 20 undescribed species.

The *Actia* fauna of the Old World is much better known than its New World counterpart, though undescribed species undoubtedly live in all regions, particularly the Australian. Distributions are listed in Crosskey (1973, 1976a, 1980) for species of Australia and the Oriental and Afrotropical regions, respectively. There are no adequate keys to aid in the identification of the numerous species of these three regions except for Dear and Crosskey's (1982) key to Philippine species. Malloch's (1930b) key to the Oriental species is long outdated and Mesnil's (1954) key to *Actia* (as *Entomophaga*) species of the upper Congo area only includes about half of the described Afrotropical species.

Palearctic *Actia* are the best studied: most European species can be identified using Mesnil's keys (1963a, 1975: 1399), though species described later by Shima (1970c) and Richter (1974, 1976a, 1980) from Japan and central Asia must be identified from descriptions. Known distributions of several Palearctic *Actia* species have been extended beyond Europe to Israel by Kugler (1979) and to central or eastern Asia by Herting (1968b, 1973), Richter (1971, 1975, 1976a,b, 1980, 1981, 1986) and Richter and Khitsova (1982). The ranges of all 13 Palearctic species are summarized in Herting (1984) and Norwegian *Actia* are listed in Rognes (1986).

List of described species included in *Actia*

A *antiqua* (Mesnil), 1954: 31 (*Entomophaga*). Holotype male, Zaire: Bambesa (MRAC). Holotype examined.

N *autumnalis* (Townsend), 1917: 122 (*Actiopsis*). Holotype female, USA: Maryland, Grove Hill (USNM). Holotype examined.

O *brunnea* Malloch, 1930b: 136. Holotype female, Malaysia: Malaya, Kedah Peak (BMNH). Holotype examined.

A *chrysocera* Bezzi, 1923a: 96. Holotype male, Seychelles: Long Island (BMNH). Holotype examined.

A *ciligera* (Mesnil), 1954: 29 (*Entomophaga*). Holotype female, Zaire: L. Kivu (MRAC). Holotype examined.

O *completa* Malloch, 1930b: 139. Holotype male, Malaysia: Malaya, Selangor (BMNH). Holotype examined.

P *crassicornis* (Meigen), 1824: 351 (*Tachina*). Holotype male, no locality data (MNHN).

    syn.   *bicolor* (Macquart), 1834: 312 (*Thryptocera*). Type, France: Lille (lost).— Herting, 1976: 3.

                flavipalpis (Macquart), 1848: 135 (*Thryptocera*). Holotype female, Switzerland: near Zurich (ETH).— Herting, 1976: 5.

                nigripalpis (Robineau-Desvoidy), 1851: 182 (*Thryptocera*). Holotype female (not male), France (MNHN).— Herting, 1974: 19.

                palpalis (Rondani), 1859: 14 (*Thryptocera*). Lectotype female (by designation of Herting, 1969a: 198), Italy: Parma (MZF).— Herting, 1969a: 198.

                claripennis (Robineau-Desvoidy), 1863: 716 (*Thryptocera*). Holotype female, France (MNHN).— Herting, 1974: 19.

                scutellaris (Rondani), 1865: 195 (*Thryptocera*). Holotype male, Italy: Parma (MZF).— Herting, 1969a: 200.

A *cuthbertsoni* Curran, 1933c: 162. Holotype male, Zimbabwe: Gatooma (AMNH).

    syn.   *cuthbersoni*. Incorrect subsequent spelling of *cuthbertsoni* Curran (Mesnil, 1977a: 83).

U *darwini* Malloch, 1929b: 334. Holotype male, Australia: Northern Territory, Darwin (SPHTM). Holotype examined.

    syn.   *brevis* Malloch, 1930a: 309. Holotype male, Australia: New South Wales, Sydney (SPHTM). Holotype examined. **New synonymy.**

O *deferens* Malloch, 1930b: 130. Holotype female (head lost), Malaysia: Malaya, Kedah Peak (BMNH). Holotype examined.

N *diffidens* Curran, 1933a: 5. Holotype male, Canada: Nova Scotia, Kentville (CNC). Holotype examined.

P *dubitata* Herting, 1971: 12. Holotype female, Switzerland: Delémont (SMNS;

not located, possibly lost). Paratype examined.

U *eucosmae* Bezzi, 1926: 239. Holotype female, Australia: Queensland, Milton Farm (published as "Brisbane") (BMNH). Holotype examined.

A *exsecta* Villeneuve, 1936: 416. Two male syntypes, Uganda: Kampala (1 in BMNH). Syntype examined.

A *fallax* (Mesnil), 1954: 29 (*Entomophaga*). Holotype female, Zaire: near Rweru (MRAC). Holotype examined.

O *fulvicauda* Malloch, 1935: 680. Holotype male, Malaysia: Malaya, Selangor (BMNH). Holotype examined.

A *gratiosa* (Mesnil), 1954: 34 (*Entomophaga*). Holotype male, Zaire: L. Kivu (MRAC). Holotype examined.

A *hargreavesi* Curran, 1933c: 160. Holotype female (head missing), Uganda: Kampala (BMNH). Holotype examined.

    syn.   *comitata* Villeneuve, 1936: 416. Four male and 2 female syntypes, Uganda: Kampala (BMNH).— Crosskey, 1980: 852. Syntypes examined.

P *infantula* (Zetterstedt), 1844: 1047 (*Tachina*). Six syntypes, Sweden: Skåne (UZI).

    syn.   *antennalis* (Rondani), 1859: 16 (*Thryptocera*). Four syntypes, Italy: Appennines (MZF).— Herting, 1969a: 190.

            aristalis (Rondani), 1865: 194 (*Thryptocera*). Two syntypes, Italy: Appennines (MZF).— Herting, 1969a: 190.

            villeneuvii (Strobl *in* Czerny and Strobl), 1909: 221 (*Thryptocera* (*Actia*)). Syntypes, Spain: Elche (NMBA).— Mesnil, 1963a: 817.

            villeneuvei. Incorrect subsequent spelling of *villeneuvii* Strobl (Mesnil, 1963a: 817).

N *interrupta* Curran, 1933a: 6. Holotype male, USA: New York, Tuxedo (AMNH). Holotype examined.

P *jocularis* Mesnil, 1957: 47. Holotype male, Japan: Tokura (CNC). Holotype examined.

P *lamia* (Meigen), 1838: 254 (*Roeselia*). Neotype male (by designation of O'Hara, 1985: 95), France: Saint-Sauveur (MNHN). Neotype examined.

    syn.   *pilipennis* Robineau-Desvoidy, 1830: 86 (junior homonym of *A. pilipennis* (Fallén); replaced by *A. lamia* (Meigen) under Article 60 of the I.C.Z.N.). Lectotype male (by designation of O'Hara, 1985: 95), France: Saint-Sauveur (MNHN). Lectotype examined.

            frontalis (Macquart), 1845: 289 (*Thryptocera*). Replacement name for *A. pilipennis* Robineau-Desvoidy, 1830 (objective synonym).

            obscurella Robineau-Desvoidy, 1851: 187. Syntypes, France (MNHN).— Herting, 1974: 19.

            vitripennis Rondani, 1859: 19. Replacement name for *A. pilipennis* Robineau-Desvoidy, 1830 (objective synonym).

lamina. Incorrect subsequent spelling of *lamia* Meigen (Schiner, 1862: 518).

U   *lata* Malloch, 1930a: 307. Holotype male, Australia: New South Wales, Sydney (SPHTM). Holotype examined.

A   *linguata* Mesnil, 1968: 10. Holotype male, South Africa: Cape Town (BMNH). Holotype examined.

A   *longilingua* (Mesnil), 1954: 36 (*Entomophaga*). Holotype male, Zaire: Rutshuru (MRAC). Holotype examined.

O   *magnicornis* Malloch, 1930b: 133. Holotype male, Malaysia: Selangor (BMNH). Holotype examined.

P   *maksymovi* Mesnil, 1952b: 153. Holotype male, Switzerland: Engadine (not located; a female paratype from same locality is mislabelled as holotype in CNC). Paratype examined.

    syn.   *maxymovi.* Incorrect subsequent spelling of *maksymovi* Mesnil (Richter, 1975: 644 and Richter, 1976a: 572).

O   *malaisei* (Mesnil), 1953: 110 (*Crocuta* (*Siphona*)). Holotype male, Burma: Kambaiti (ZMU). Holotype examined.

O   *mimetica* Malloch, 1930b: 143. Holotype female, Malaysia: Malaya, Kedah Peak (BMNH). Holotype examined.

P   *mongolica* Richter, 1976a: 572. Holotype male, Mongolia: Eastern aimak (ZIL). Holotype examined.

A   *munroi* Curran, 1927a: 322. Holotype female, South Africa: Barberton (PPRI). Holotype examined.

P   *nigra* Shima, 1970c: 184. Holotype male, Japan: Hokkaido, Mt. Satsunai, Pirikapetanu (BLKU). Paratype examined.

A   *nigrapex* Mesnil, 1977a: 83. Holotype male, Madagascar: Amber Mtn. (MNHN).

O   *nigriventris* Malloch, 1935: 680 (as variety of *Actia eucosmae* Bezzi). Holotype female (abdomen lost), Malaysia: Malaya, Selangor (BMNH). Holotype examined.

P   *nigroscutellata* Lundbeck, 1927: 462. Two male and 2 female syntypes, Denmark: Tisvilde (ZMUC). Syntypes examined.

A   *nitidella* Villeneuve, 1936: 417. Holotype female, Uganda: Kampala (BMNH). Holotype examined.

S   *nitidiventris* Curran, 1933a: 4. Holotype female, Panama: Barro Colorado Is. (AMNH). Holotype examined.

P   *nudibasis* Stein, 1924: 135. Four syntypes, German Democratic Republic: Crimmitschau (ZMHU).

    syn.   ? *resinellae* (Schrank), 1781: 478 (*Musca*). Type(s), Austria (lost).— Mesnil, 1963a: 825.

O   *oblimata* Mesnil, 1957: 45. Holotype male, Burma: Kambaiti (ZMU). Holotype examined.

U   *painei* Crosskey, 1962: 173. Holotype male, New Britain: Rabaul (BMNH). Holotype examined.

A   *pallens* Curran, 1927a: 322. Holotype female, South Africa: Natal, Durban (PPRI). Holotype examined.

P   *pamirica* Richter, 1974: 1268. Holotype male, USSR: Pamir, Debastia (ZIL). Holotype examined.

U   *parviseta* Malloch, 1930a: 308. Holotype male, Australia: New South Wales, Sydney (SPHTM). Holotype examined.

O   *pellex* (Mesnil), 1953: 111 (*Crocuta* (*Siphona*)). Holotype female, Burma: Kambaiti (ZMU). Holotype examined.

O   *perdita* Malloch, 1930c: 333. Holotype male (head lost), Malaysia: Malaya, Selangor (BMNH). Holotype examined.

O   *philippinensis* Malloch, 1930b: 134. Holotype female (head and abdomen lost), Philippines: Luzon, Benguet (USNM). Holotype examined.

A   *picipalpis* (Mesnil), 1954: 33 (*Entomophaga*). Holotype female (not male), Zaire: Rutshuru (MRAC). Holotype examined.

P   *pilipennis* (Fallén), 1810: 273 *(Tachina)*. Lectotype male (by designation of Crosskey, 1974: 302), Sweden (NRS).

    syn.   *broteas* (Walker), 1849: 763 (*Tachina*). Holotype male, England (BMNH).— Crosskey, 1974: 277. Holotype examined.
    flavisquamis (Robineau-Desvoidy), 1851: 181 (*Thryptocera*). Syntypes, France (MNHN).— Herting, 1974: 19.
    humeralis (Robineau-Desvoidy), 1851: 183 (*Thryptocera*). Holotype female, France (lost).— Herting, 1984: 123.
    exscensa (Walker), 1853: 66 (*Tachina*). Holotype female, England (BMNH).— Crosskey, 1974: 283. Holotype examined.
    nigrifrons (Robineau-Desvoidy), 1863: 714 (*Thryptocera*). Holotype male, France (MNHN).— Herting, 1974: 19.
    bigoti (Millière), 1864: 385 (*Morinia*). Type(s), France (lost).— Herting, 1984: 123.
    reducta Villeneuve, 1920: 66 (as variety of *A. pilipennis* (Fallén), though Villeneuve's description of *A. pilipennis* actually refers to *A. nudibasis* (Herting, *in litt.*)). Type(s), no locality given (not located).

O   *pokharana* Shima, 1970b: 275. Holotype male, Nepal: Pokhara (BPBM).

U   *pulex* Baranov, 1938: 410. Lectotype male (by designation of Sabrosky and Crosskey, 1969: 35), Solomon Islands: Tulagi (BMNH). Lectotype examined.

U   *quadriseta* Malloch, 1936: 20. Holotype female, Australia: New South Wales, Nyngan (SPHTM). Holotype examined.

A   *rejecta* Bezzi *in* Bezzi and Lamb, 1926: 569. Holotype male (not female), Rodriguez Is. (BMNH). Holotype examined.

A   *rubiginosa* (Mesnil), 1954: 35 (*Entomophaga*). Holotype male, Zaire: Mokoto (MRAC). Holotype examined.

N *rufescens* (Greene), 1934: 34 (*Actiopsis*). Holotype female, USA: South Dakota (USNM). Holotype examined.

A *russula* Mesnil, 1977a: 84. Holotype male, Madagascar: Joffreville (MNHN).

O *siphonosoma* Malloch, 1930b: 136. Holotype male, Malaysia: Malaya, Selangor (BMNH). Holotype examined.

O *takanoi* Baranov, 1935: 557. Lectotype female (by designation of Sabrosky and Crosskey, 1969: 35), Philippines: Luzon, Los Baños (USNM). Lectotype examined.

P *tarsata* Richter, 1980: 541. Holotype female, USSR: Chitinskaya Oblast, Adrianovka (ZIL). Holotype examined.

A *triseta* (Mesnil), 1954: 32 (*Entomophaga*). Holotype male, Rwanda: near Rweru (MRAC). Holotype examined.

A *vulpina* (Mesnil), 1954: 34 (*Entomophaga*). Holotype male, Zaire: Bambesa (MRAC). Holotype examined.

O *yasumatsui* Shima, 1970b: 273. Holotype male, Hong Kong: Kowloon, Taipokau (BPBM).

Nomen dubium

P *rubrifrons* (Robineau-Desvoidy), 1830: 87 (*Ceromya*). Type(s), France (lost).—see Herting, 1974: 18.

Nomina nuda

N *labellata* Kamran, 1980: 52.

N *pauciseta* Kamran, 1980: 52.

List of examined, undescribed, species included in *Actia*

Actia nr. *parviseta*: One female from SE Queensland, Australia (DPI).
Actia Australia sp. 1 (=*A. darwini*?): Males and females from Queensland (DPI).
Actia Australia sp. 2: One male from Mt. Lewis, Queensland (DPI).
Actia Australia sp. 3: One male, one female from Rockhampton, Queensland (DPI).
Actia Australia sp. 4: Two males, one female from Mt. Tamborine, Queensland (DPI).
Actia Australia sp. 5: Males and females from Queensland (CNC, DPI).
Actia Jamaica sp. 1: Males and females from St. Catherine (USNM).
Actia Liberia sp. 1: One male from Liberia (USNM).
Actia Mexico sp. 1: One male from San Cristobal, Chiapas (CNC).
Actia Nepal sp. 1: Males from Nepal (CNC).
Actia Nepal sp. 2: One male from Kathmandu (CNC).
Actia New World spp. 1-19: These species are presently under revision by O'Hara and Shima.
Actia Uganda sp. 1: One male from Ankole (USNM).

Genus *Peribaea* Robineau-Desvoidy
Figs. 11-12, 27, 60-61, 87-88, 120-121, 139, 153-156, 161.

Herbstia Robineau-Desvoidy, 1851: 184 (junior homonym, preoccupied by *Herbstia* Edwards, 1834). Type-species, *H. tibialis* Robineau-Desvoidy, 1851 (monotypy).

Peribaea Robineau-Desvoidy, 1863: 720. Type-species, *P. apicalis* Robineau-Desvoidy, 1863 (by designation of Coquillett, 1910: 587).

Strobliomyia Townsend,, 1926c:31. Type-species, *Thryptocera fissicornis* Strobl, 1910 (original designation).

Eogymnophthalma Townsend, 1926a: 35. Type-species, *E. orientalis* Townsend, 1926 (original designation) = *Tachina orbata* Wiedemann, 1830.

Talaractia Malloch, 1930a: 305 (as subgenus of *Actia*). Type-species, *Actia (Talaractia) baldwini* Malloch, 1930 (original designation).

Tararactia. Incorrect subsequent spelling of *Talaractia* Malloch (Malloch, 1930a: 305).

Uschizactia Townsend, 1934: 248. Type-species, *Actia uniseta* Malloch, 1930 (original designation).

Recognition

Species of the genus *Peribaea* are widely distributed throughout the Old World, and are easily recognized among siphonines by their possession of a strong, downwardly directed, proepimeral seta (Fig. 27). Species of *Chaetostigmoptera* Townsend and the Neaerini, and several other tachinids, also have a distinctly developed, downwardly directed, proepimeral seta (varied from weak to strong), though other differences indicate that this similarity is due to convergence. Together, *Peribaea* and *Siphona s.l.* are distinguishable from all but a very few other siphonines (and almost all other tachinids) by having the anal vein extended to the wing margin.

Description

Length: 2.5-5.0mm.

Head (Figs. 11-12).— Five frontal setae, normal arrangement. Anterior proclinate orbital seta longer than posterior one in most species. Eye of male and female subequal in size, medium to large, 0.73-0.86 head height; size in female subequal to that of male. Flagellomere 1 of male markedly varied in length, 0.39-0.75 head height; shape from linear or broad to bifid (*e.g.* figs. 3a, 4a and 5a in Shima 1970a), trifid (*P. jepsoni* and *P. trifurcata*; *e.g.* fig. 2a, *op. cit.*), or pectinate (*P. baldwini, P. cervina* and *P. pectinata*; Fig. 11 and fig. 1a, *op. cit.*). Flagellomere 1 of female simple, not bifid. Aristomere 1 short. Aristomere two 1.5-12X longer than wide (2-4X in most species). Aristomere 3 long and evenly tapered in most species, short and thickened to near tip in a few; almost bare to short plumose, in most species micropubescent. Clypeus U-shaped in most species, only slightly broadened in a few. Palpus short, clavate. Proboscis with prementum short to medium (not elongate), labella padlike.

Thorax (Fig. 27).— Prosternum setulose. Lower proepimeral seta strong and directed downward (Fig. 27). Katepisternum bare anterior to mid coxa. Lower katepisternal seta slightly shorter than or subequal in length to upper anterior seta in most species, slightly longer in a very few. Four postsutural dorsocentral setae (apparently never three). Upper part of anepisternum with single setula. Fore tibia with preapical *ad* seta much shorter than *d* seta. Mid tibia with one *ad* seta. Tarsomeres normal in size, or tarsomere 5 of fore leg elongate and broadened (only known in female of *P. lobata*); claws short in most species, medium in a very few. Wing: CuA_1 with distal portion 0.63-1.3X length of proximal portion (mean 0.84); anal vein extended to wing margin. Wing setulae: R_1 dorsally bare, or distally or entirely setulose, ventrally bare or distally setulose; R_{2+3} bare except setulose dorsally and ventrally in *P. modesta*; R_{4+5} setulose from base to beyond r-m; CuA_1 bare in almost all species (a few sparsely setulose).

Abdominal terga 1-5.— Abdomen ovoid in most species, markedly elongate in a few, and very elongate in   *P.*   *ugandana.*

T_{1+2} without median marginal setae; lateral marginal setae absent from most species, strong in a few. T_3-T_5 average in most species, with extra pair of lateral marginal setae on T_3 in a few, weak lateral discal setae on T_4-T_5 in *P. discicornis*.

Male genitalia (Figs. 60-61, 87-88, 120-121, 139).— S_5 markedly varied, inner (or posterior) margins of processes obtusely angled (Fig. 60) to almost transverse in most species, in a very few species V-shaped (Fig. 61; resembling typical *Actia* shape except median cleft more distinct); apical lobe undifferentiated to slightly differentiated; median lobe slightly to broadly rounded in most species, rather elongate and/or flattened medially or posteromedially in a few; processes moderately setulose, with three to six pair of large setae in most species. T_6 varied from small pair of lateral sclerites to single, broad, dorsally continuous sclerite. Ejaculatory apodeme with fan-shaped portion wider than hypandrial apodeme in most species, subequal in width in a very few; some species with weak ring-like sclerotized sheath basally (*e.g. P. apicalis*). Pregonite (Figs. 87-88) in profile approximately C-shaped, broad at mid length; bare. Epiphallus present or absent, where present generally narrow. Distiphallus (Figs. 120-121) large, posterior margin complete, variously incised laterally, distinctly broader than long in ventral view. Postgonite apically rounded, pointed, or turned outward. Surstylus (Fig. 139) average length to long, broad in a few species, straight to curved posteriorly; basally free from epandrium in most species (Fig. 139), fused with epandrium in a few (*e.g. P. trifurcata*); apically enlarged in some species, greatly swollen in a few, in one (?undescribed) species from Australia subapically with small medially-directed lobe. Cerci short in most species (Fig. 139), average length in a few, in profile straight along posterior margin or smoothly curved at midlength; moderately setose on basal half.

Examined male genitalia of: *P. apicalis, P. fissicornis, P. repanda, P. ?similata, P. tibialis, P. ugandana*, Africa spp. 1-4, Australia spp. 1-3, Nepal sp. 1 and Sri Lanka sp. 1. Examined published figures of: *P. fissicornis* (Andersen 1983, fig. 18), *P. hirsuta, P. illugiana, P. pectinata, P. sedlaceki, P. trifurcata* (all five in Shima 1970a, figs. 1-5), *P. insularis* (Shima 1970c, figs. 1, 3a), *P. alternata* and *P. orbata* (both in Shima 1981, figs. 1 and 3).

Female genitalia (Figs. 153-156).— Varied from short and unmodified (Fig. 153) to extremely elongate (Figs. 155-156). S_6 bare or with very short hairs; in primitive forms S_6 and S_7 flat and wider than long, in derived forms both sterna slightly to sharply keeled medially and pointed posteriorly in most species, in very specialized forms both sterna elongate and tip of S_7 extended over cerci, with intersegmental membrane similarly elongate (Figs. 155-156); S_7 without anterior apodeme. T_6 distinctly developed and enclosing spiracles of segment 6; dorsally continuous or discontinuous. T_7 present as lateral sclerites in unmodified forms, fused with S_7 in some derived forms with S_7 elongate (Figs. 154-156); enclosing spiracles of segment 7. S_8 bare, absent (particularly in elongate forms) to average-sized, flat sclerite. T_{10} absent from some species, present as a small to medium median sclerite in others.

Examined female genitalia of: *P. fissicornis, P. tibialis, P. ugandana*, Africa spp. 2-5 and Australia spp. 1,3. Examined published figures of: *P. alternata, P. orbata* (both in Shima 1981, fig. 2) and *P. tibialis* (Andersen 1983, fig. 4).

Taxonomic changes

Identity of Tachina orbata Wiedemann.— The type of *Tachina orbata* Wiedemann (1830: 336) is lost. Crosskey (1967) designated a neotype for this species, believing *T. orbata* to be a widespread Old World species of *Peribaea*. According to Mesnil (*in litt.*), the original description of *T. orbata* refers to a neaerine. If one were to accept this opinion and invalidate Crosskey's neotype (on the basis of an incorrect neotype designation), then *P. aegyptia* would become the valid name for this *Peribaea* species. However, in the interests of nomenclatural stability, Crosskey and Shima plan to submit a proposal to the International Commission on Zoological Nomenclature requesting that Crosskey's (1967) neotype be retained for the name *Tachina orbata* Wiedemann (Crosskey *in litt.*). Current usage of *orbata* as a valid species of *Peribaea* is followed herein.

Status of Peribaea subaequalis (Malloch).— Malloch described *P. monticola*, *P. rotundipennis* and *P. subaequalis* from specimens collected in the Cuernos Mts. on Negros Island in the Philippines. The first two names were synonymized with *P. orbata* by Crosskey (1966: 107), while the third has continued to be cited as valid (Crosskey, 1976: 214). I examined all three of Malloch's types along with specimens of *P. orbata*, and found no substantial difference among them. Unfortunately, Malloch's type specimens are not ideal for comparison because all three lack heads, and two are females while the third is a male. Nevertheless, the fact that Malloch's types were collected from the same locality (dates unknown) and are similar to one another and to specimens of *P. orbata* in such important characteristics as wing vein setulation and abdominal coloration strongly suggests that they are all conspecific. (Even Malloch stated that his specimens "may ultimately prove to be mere variations within a single species" (1930b: 142).) The one difference, anal vein not extended to wing margin in the type of *P. subaequalis*, is very rare in *Peribaea* and not typical of any known species, so probably represents an aberration in this specimen (even the paratypes of *P. subaequalis* have the anal vein reaching wing margin). For all these reasons I feel confident in adding *P. subaequalis* to the list of synonyms of the widespread species *P. orbata*.

Hosts

Hosts of *Peribaea* species belong to several families of Microlepidoptera and Macrolepidoptera (Table 2). The most commonly parasitized group is the Noctuoidea, accounting for half the total records.

Adult females of *Peribaea* species are thought to larviposit directly on their hosts (Herting 1957). Presumably the elongate ovipositor of some *Peribaea* species is an adaptation to this behavior.

Phylogenetics

The monophyly of *Peribaea* is well established (Andersen 1983: 10). Adults possess externally a strong, downwardly directed, proepimeral seta (Fig. 27). This state is unique to *Peribaea* among siphonines, though is convergently, and often more weakly, developed in species of *Chaetostigmoptera* Townsend and the Neaerini, and several other tachinids. The distiphallus is varied in shape among *Peribaea* species, though its sclerotized posterior surface is a shared characteristic and is hypothesized as a synapotypy; the partially unsclerotized posterior surface in all but a very few other (unrelated) siphonines (see Table 1) is interpreted as plesiotypic. Sternum 8 in the female genitalia is bare in all examined *Peribaea* species, though several derived species lack this sclerite entirely (Figs. 154-156). A bare, unsclerotized sternum 8 is considered synapotypic of the genus, and absence of sternum 8 is interpreted as a more derived condition (sternum 8 convergently lost in a few other siphonines; see Table 1).

First instars of *Peribaea* species are characterized by an apically narrowed or hook-like labrum (Fig. 161; also see O'Hara in press "a"). A hatchet-like labrum characterizes more primitive siphonines (with the known exception of *Ceromya silacea*, Fig. 159), so the shape of the labrum in *Peribaea* species is interpreted as derived.

Geographic distribution

Forty-five described species are recognized in *Peribaea*, all are restricted to the Old World. Greatest diversity, accounting for almost half the described species, is recorded from the Afrotropical region (particularly the upper Congo area, as a result of Mesnil's work on the siphonines of that area; distributions in Crosskey 1980). More modest diversity is found in the three other Old World regions. Oriental species are listed in Crosskey (1976a; Philippine species keyed in Dear and Crosskey 1982) and Australian species in Crosskey (1973) and Shima (1970a, with key to Papuan species; 1981). Most Palearctic *Peribaea* species are redescribed and keyed in Mesnil (1963a; also key to separate *P. apicalis* and *P. tibialis* in Herting 1968a). Other records for Palearctic species are given in Mesnil and Pschorn-Walcher (1968), Herting (1968b, 1969b), Crosskey (1976b), Kugler (1979), Karczewski (1983), Mihályi and Weinberg (1984), Richter (1971, 1975, 1976a, 1980, 1981, 1986) and Rognes (1986), and summarized in Herting (1984).

I suspect that the preponderance of described species in the Afrotropical region accurately reflects the true pattern of *Peribaea* diversity. Presence of ten species in the Australian region (including one on the Solomon Islands), seven species on Madagascar (Mesnil 1977a) and one each on Mauritius and Seychelles Islands, indicates that the dispersal power of some members of this genus are as great as in other siphonine genera that are distributed worldwide. It is therefore puzzling that *Peribaea* has not reached the New World. Hosts do not seem to be the limiting factor, as many host genera are Holarctic or cosmopolitan in distribution.

List of described species included in *Peribaea*

U   *alternata* Shima, 1981: 445. Holotype male, New Guinea: Wau, Mt. Kaindi (BPBM). Paratype examined.
A   *annulata* (Mesnil), 1954: 21 (*Strobliomyia*). Holotype male, Zaire: Rwankwi (MRAC). Holotype examined.
A   *anthracina* Mesnil, 1977a: 81. Holotype male, Madagascar: Belazao (MNHN).
P   *apicalis* Robineau-Desvoidy, 1863: 721. Holotype male (head and abdomen lost), France: Saint Sauveur (MNHN).
U   *argentifrons* (Malloch), 1930a: 309 (*Actia*). Holotype male, Australia: New South Wales, Sydney (SPHTM). Holotype examined.
   syn.   *angustifrons*. Incorrect subsequent spelling of *argentifrons* Malloch (Hardy, 1959: 213).

U *baldwini* (Malloch), 1930a: 306 (*Actia* (*Talaractia*)). Holotype male, Australia: Queensland, Palm Is. (SPHTM). Holotype examined.

A *cervina* (Mesnil), 1954: 18 (*Strobliomyia*). Holotype male, Zaire: Rutshuru (IRSN). Holotype examined.

A *clara* (Mesnil), 1954: 21 (*Strobliomyia*). Holotype male, Zaire: Katanga, Kalabi (MRAC). Holotype examined.

A *compacta* (Curran), 1927a: 324 (*Actia*). Holotype male (head lost), South Africa: East London (PPRI). Holotype examined.

P *discicornis* (Pandellé), 1894: 109 (*Thryptocera*). Holotype male, France: Pyrenees, Tarbes (IRSN).

A *ferina* (Mesnil), 1954: 17 (*Strobliomyia*). Holotype male, Rwanda: Kibga (MRAC). Holotype examined.

P *fissicornis* (Strobl), 1910: 139 (*Thryptocera*). Holotype male (not female), Austria: "Styria" (NMBA).

A *gibbicornis* (Mesnil), 1954: 19 (*Strobliomyia*). Holotype male, Zaire: Rutshuru (IRSN). Holotype examined.

U *hirsuta* (Shima), 1970a: 269 (*Strobliomyia*). Holotype male, New Guinea: Popondetta (BPBM).

O *hyalinata* (Malloch), 1930b: 138 (*Actia*). Holotype female (not male), Malaysia: Malaya, Selangor (BMNH). Holotype examined.

U *illugiana* (Shima), 1970a: 265 (*Strobliomyia*). Holotype male, New Britain: Gazelle Peninsula, Illugi (BPBM).

O *insularia* (Shima), 1970c: 179 (*Strobliomyia*). Holotype male, Japan: Ryukyu Islands, Amami Is., Tokunoshima (BLKU).

A *jepsoni* (Villeneuve), 1937: 2 (*Strobliomyia*). Holotype male, Mauritius (CNC). Holotype examined.

P *leucopheae* (Mesnil), 1963b: 33 (*Strobliomyia*). Holotype female, USSR: Tadjikistan, Varzoba (ZIL). Holotype examined.

A *lobata* Mesnil, 1977a: 80. Holotype male, Madagascar: Manjakatatompo (MNHN).

A *longiseta* (Villeneuve), 1936: 417 (*Actia*). Holotype female, Uganda: Kampala (BMNH). Holotype examined.

O *malayana* (Malloch), 1935: 678 (*Actia*). Holotype male (abdomen lost), Malaysia: Malaya, Selangor (BMNH). Holotype examined.

A *mitis* (Curran), 1927a: 323 (*Actia*). Syntypes, South Africa: Barberton (PPRI). Syntypes examined.

A *modesta* (Mesnil), 1954: 14 (*Strobliomyia*). Holotype male, Zaire: Rutshuru (MRAC). Holotype examined.

O,P,A,U *orbata* (Wiedemann), 1830: 336 (*Tachina*). Neotype female (by designation of Crosskey, 1967: 106), India: Assam, Azra (BMNH). Lectotype examined.

      syn.   *aegyptia* (Villeneuve), 1912: 508 (*Gymnopareia* (*Actia*)). Lectotype

male (by designation of Crosskey, 1966: 108), Egypt: Qaliub (BMNH).— Crosskey, 1976a: 214. Lectotype examined.

orientalis (Townsend), 1926a: 35 (*Eogymnophthalma*). Lectotype male (by fixation of Townsend, 1940: 213), Indonesia: Sumatra, Fort de Kock (ZMA).— Crosskey, 1966: 107. Lectotype examined.

nigripes (Curran), 1927c: 6 (*Actia*). Holotype male, Zaire: Boma (AMNH).— Crosskey, 1980: 853. Holotype examined.

nigritula (Malloch), 1930a: 309 (*Actia*). Holotype female, Australia: Queensland, Cairns (SPHTM).— Crosskey, 1966: 107. Holotype examined.

subaequalis (Malloch), 1930b: 142 (*Actia*). Holotype male (head lost), Philippines: Negros, Cuernos Mtns. (USNM). Holotype examined. **New synonymy**.

monticola (Malloch), 1930b: 143 (*Actia*). Holotype male (head lost), Philippines: Negros, Cuernos Mtns. (USNM).— Crosskey, 1966: 107. Holotype examined.

rotundipennis (Malloch), 1930b: 143 (*Actia*). Holotype female (head lost), Philippines: Negros, Cuernos Mtns. (USNM).— Crosskey, 1966: 107. Holotype examined.

sororcula (Mesnil), 1954: 16 (*Strobliomyia*). Holotype female, Zaire: Rutshuru (MRAC).— Crosskey, 1976a: 214. Holotype examined.

P   *palaestina* (Villeneuve), 1934: 57 (*Actia*). Holotype female, Israel: Rehoboth (SMNS). Holotype examined.

    syn.   *alipes* (Villeneuve), 1942b: 134 (*Actia*). Holotype female, Egypt: Assuan (CNC).— Herting, 1982: 8. Holotype examined.

U   *pectinata* (Shima), 1970a: 261 (*Strobliomyia*). Holotype male, New Britain: Gazelle Penn., Illugi (BPBM).

U   *plebeia* (Malloch), 1930a: 310 (*Actia*). Holotype male, Australia: New South Wales, Coramba (SPHTM). Holotype examined.

    syn.   *plebia*. Incorrect subsequent spelling of *plebeia* Malloch (Hardy, 1959: 213).

A   *pulla* Mesnil, 1977a: 82. Holotype male, Madagascar: Ambato-Boeni (MNHN).

A   *repanda* (Mesnil), 1954: 16 (*Strobliomyia*). Holotype male, Zaire: nr. Rwindi, Ndeko (MRAC). Holotype examined.

A   *rubea* Mesnil, 1977a: 82. Holotype female, Madagascar: Amber Mtn. (MNHN).

U   *sedlaceki* (Shima), 1970a: 267 (*Strobliomyia*). Holotype male, New Guinea: Popondetta (BPBM).

O   *setinervis* (Thomson), 1869: 519 (*Thryptocera*). Holotype female, China (NRS).

O,P *similata* (Malloch), 1930b: 137 (*Actia*). Holotype male, Malaysia: Malaya, Selangor (BMNH). Holotype examined.

A   *spoliata* (Bezzi), 1923a: 95 (*Actia*). One male and 1 female syntype, Seychelles

Islands (BMNH). Syntypes examined.

U *stiglinae* (Bezzi), 1928: 204 (*Actia*). Holotype male (not female), Fiji: Lautoka (BMNH). Holotype examined. **New combination**, moved from *Actia*.

O,A *suspecta* (Malloch), 1924: 409 (*Actia*). Holotype male (not female), India: Bihar, Pusa (BMNH). Holotype examined.

      syn.   *nana* (Curran), 1928: 237 (*Actia*). Holotype female, Uganda: Kampala (BMNH).— Crosskey, 1976a: 214. Holotype examined.

P,A *tibialis* (Robineau-Desvoidy), 1851: 185 (*Herbstia*). Holotype male, France: Saint Sauveur (lost).

      syn.   *flavicornis* Robineau-Desvoidy, 1863: 721. Holotype female, France: Lozère (MNHN).— Herting, 1974: 19.

            minuta Robineau-Desvoidy, 1863: 722. Holotype female, France (MNHN).— Herting, 1974: 19.

A *timida* (Mesnil), 1954: 18 (*Strobliomyia*). Holotype male, Zaire: Rutshuru (MRAC). Holotype examined.

U *trifurcata* (Shima), 1970a: 263 (*Strobliomyia*). Holotype male, New Guinea: Popondetta (BPBM).

A *ugandana* (Curran), 1933c: 161 (*Actia*). Holotype male, Uganda: Kampala (BMNH). Holotype examined.

O *uniseta* (Malloch), 1930b: 129 (*Actia*). Holotype male (head lost), Malaysia: Malaya, Selangor (BMNH). Holotype examined.

P *ussuriensis* (Mesnil), 1963a: 807 (as subspecies of *Strobliomyia hyalinata* (Malloch)). Holotype male, USSR: Ussuri, Sučan (ZIL). Holotype examined.

A *vidua* (Mesnil), 1954: 15 (*Strobliomyia*). Holotype male, Zaire: Rutshuru (MRAC). Holotype examined.

List of examined, undescribed, species included in *Peribaea*

Peribaea Africa sp. 1: Two males from Ngong, Kenya (USNM).
Peribaea Africa sp. 2: One male and one female from Ankole, Uganda (USNM).
Peribaea Africa sp. 3: One male and one female from Archer's Post, Kenya (CAS).
Peribaea Africa sp. 4: Males and females from Natal, South Africa (USNM).
Peribaea Africa sp. 5: One female from Kruger Nat. Pk., South Africa (USNM).
Peribaea Australia sp. 1: Males and females from Queensland (DPI).
Peribaea Australia sp. 2: One male and one female from Kairi, Queensland (DPI).
Peribaea Australia sp. 3: Males and females from Queensland (DPI).
Peribaea Nepal sp. 1: Three males from Lothar (CNC).
Peribaea Sri Lanka sp. 1: One male from Colombo (CAS).

Genus *Siphona* Meigen *sensu lato*
Figs. 13-20, 22, 24-26, 28, 30, 32, 34, 36, 38, 43-46, 62-70, 89-106, 122-136,
140-144, 162-163.

Recognition

Siphona Meigen, as considered here in the broad sense, is a diverse, monophyletic group of cosmopolitan distribution. Adults are morphologically varied, but all are characterized by the anal vein extended to the wing margin at least as a sharply creased fold (Fig. 22). This state is also shared by *Peribaea* species, but these are easily recognized by their two strong and opposed proepimeral setae (one strong proepimeral seta in *Siphona s.l.* species and other siphonines, *cf.* Figs. 27 and 28).

Three known Old World *Actia* species are easily confused with *Siphona s.l.* species because they have the anal vein extended to the wing margin. They differ from members of *Siphona s.l.* in their possession of a partial to complete row of katepisternal hairs and distinctive *Actia*-type male genitalia (see Recognition section of *Actia*).

Though not very useful for general identification purposes, two features of first instars are diagnostic (and synapotypic) of *Siphona s.l.* species; both on the ventral surface of the abdomen on segments 6 and 7 (see O'Hara in press "a"). Segment 6 in *Siphona s.l.* species is equipped posteriorly with from two, to a row of about 10, large spinules or hooks (Figs. 162-163). Other siphonines are bare in this region or have tiny spinules (Figs. 158-161) with the exception of *Ceromya* Australia sp. 3. *S. (Aphantorhaphopsis)* Uganda sp. 1 is the only known *Siphona s.l.* species without the typical condition of the genus. The spinulose condition on the ventral surface of segment 7 posteriorly also distinguishes almost all *Siphona s.l.* species from other siphonines. With the exception of a few species (see Table 1), *Siphona s.l.* species (Figs. 163) have a single dominant row of spinules in this position and other siphonines (Figs. 158-161) have two or more even or uneven rows of spinules (*S. (Pseudosiphona)* species have the latter condition, as exemplified here by *S. (P.)* sp. 14, Fig. 162).

Key to adults of the subgenera of *Siphona sensu lato*

(See section entitled "Review of major keys to genera and subgenera of the Siphonini" for information about how other authors have keyed (and classified) the following taxa.)

1.   Mid tibia lacking *ad* seta (Fig. 38); aristomere 1 at least 2X
        longer than wide, subequal in length to aristomere 2 (Fig. 15);
        2-3mm long (five species; western North America)....................
        ....*S. (Baeomyia* O'Hara), p. 97
1'.   Mid tibia with one or two *ad* seta on lower half (Fig. 37);

aristomere 1 shorter than aristomere 2, in most species shorter than wide (Figs. 13-14, 16-20); average-sized specimens of all but a very few species longer than 3mm 2

2. (1') Maxillary palpus cylindrical to tip, markedly reduced to average length (Fig. 16)... 3

2'. Maxillary palpus clavate apically, short to long (Figs. 1-15, 17-20). 4

3. (2) Distiphallus laterally incised and posterolateral arm clearly developed (Fig. 127); pregonite bare in Mauritius sp. 1, with long seta posteriorly in other species (Fig. 94) (Afrotropical, Nearctic, Palearctic and Oriental regions).....................................
....*S. (Ceranthia* R.-D.), p. 99

3'. Distiphallus not laterally incised and without posterolateral arm; pregonite bare (two Australian species, Australia sp. 1 and New Guinea sp. 1) ....
two undescribed species of *S. (Aphantorhaphopsis* Tnsd.), p. 92

4. (2') Proboscis with prementum and labella elongate, labella slightly longer than prementum and in most species longer than eye height (Figs. 25-26); pregonite of male genitalia without seta posteriorly and lacking spinules apically (Fig. 96); female genitalia unmodified (Figs. 43, 45) except in *S. melanura* (over 80 described species; cosmopolitan) .... *S. (Siphona* Mg.), p. 108

4'. Proboscis with prementum and labella varied in length, labella in most species padlike to slightly lengthened (Figs. 13-15, 17-19, 23-24), in a very few species as long as prementum (Fig. 20); male genitalia varied, in almost all species in which labella are as long as prementum the pregonite has a seta posteriorly and/or tiny spinules apically (Figs. 89-95, 97-98, 100, 102-106); female genitalia varied... 5

5. (4') Old World in distribution (a polyphyletic group of 21 described and many new species) ....
....................................*S. (Aphantorhaphopsis* Townsend), p. 92

5'. New World in distribution 6

6. (5') Distiphallus in profile with parallel anterior and posterior margins, with or without spines apically (Figs. 122-123); pregonite long and slender with tiny spinules apically (Fig. 89); cerci broadened in posterior view (Fig. 142); head as in Fig. 13, with labella varied from padlike to moderately lengthened; body mostly yellow with sparse abdominal pruinosity; wing vein R_{4+5} setulose from base to beyond crossvein *r-m* (*S. singularis* complex and one new species; Neotropical) ....
.... *S. (Actinocrocuta* Townsend), p. 87

6'. Male genitalia varied, with not more than one of above states;

externally varied, but a very few species with above states 7

7.   (6')   Distiphallus in profile narrow on apical half and with or without enlarged spines apically or anteriorly (Fig. 130); pregonite without spinules anterolaterally (Figs. 97-98); male sternum 5 with apex of apical lobe curved inward (similar to Figs. 62-63); proboscis with labella elongate, 0.7-0.9 prementum length (Figs. 18, 24); wing vein R_{4+5} not setulose beyond crossvein *r-m* (three described and at least 13 new species; western United States and Neotropics) ....
....*S. (Siphonopsis* Townsend), p. 120

7'.   Distiphallus in profile broader on apical half than in Fig. 130 and with or without enlarged spines apically and/or anteriorly; pregonite with or without tiny spinules anterolaterally; male sternum 5 with or without apex of apical lobe curved inward; externally varied, but a few species with above states 8

8.   (7')   Pregonite (Fig. 95) with tiny spinules anterolaterally, broad with two or more tiny setae posteriorly in most species, a few species with J-shaped pregonite or only one tiny seta posteriorly; distiphallus triangular in profile in most species (Fig. 128); cerci sharply inflexed at midlength in most species (Fig. 140); head habitus varied, but most species with row of short parafacial hairs extended to lower half of eye, arista haired and proboscis with labella slightly more than half prementum length (Fig. 17) (one described and at least 18 new species; United States to northern Argentina) ....
....*S. (Pseudosiphona* Townsend), p. 103

8'.   Pregonite more slender than in Fig. 95, with not more than one seta posteriorly and with or without spinules anterolaterally; distiphallus varied, but not triangular as in Fig. 128; cerci smoothly curved to sharply inflexed; externally varied, but a very few species with above states 9

9.   (8')   Male genitalia with median lobe of sternum 5 flattened (Fig. 68), pregonite bare (no spinules or posterior seta; Fig. 99), distiphallus smoothly tapered in profile (Fig. 131), and cerci sharply inflexed at midlength; body relatively large, 4.0-5.0mm in length; also see Recognition section (one described and one new species; Ecuador and Peru) ....
....*S. (Uruactia* Townsend), p. 123

9'.   Male genitalia varied, but with not more than two of the four states above 10

10. (9')   Male genitalia with pregonite lacking spinules anterolaterally (Fig. 90; posterior seta present or absent), distiphallus tapered

in profile (Fig. 124), and cerci not sharply inflexed at midlength and of average shape (similar to Fig. 144) to slightly broadened (Fig. 143) in posterior view; body relatively small, 2.0-3.5mm in length and dark-colored; also see Recognition section (two described and at least four new species; SW United States to SE Brazil) .... *S. (Aphantorhapha* Townsend), p. 89

10'.   Male genitalia without above combination of states; externally varied (two described and over 40 new species; New World, mostly Neotropical) ....
...New World *Siphona s.l.* species unplaced to subgenus, p. 125 [See descriptive sections on three species groups and unplaced species of New World *Siphona s.l.*]

Siphona (subgenus *Actinocrocuta* Townsend)
Figs. 13, 62, 89, 122-123, 142.

Actinocrocuta Townsend, 1935: 228. Type-species, *A. chaetosa* Townsend, 1935 (original designation) = *Tachina singularis* Wiedemann, 1830. **New subgeneric status** in *Siphona* Meigen.

Recognition

Adults of this Neotropical group of few species cannot be distinguished from all other *Siphona s.l.* species except by features of the male genitalia, though the following external characteristics are shared by the known species: yellow overall except for varied amounts of reddish brown at femoral-tibial articulations, surrounding marginal setae on abdomen, and along abdominal midline; abdomen very sparsely pruinose; lower katepisternal seta at least length of upper anterior seta; three postsutural dorsocentral setae; wing vein R_{4+5} setulose from base to beyond crossvein *r-m*; and anal vein extended to wing margin. The following combination of male genitalic states is unique to *S. (Actinocrocuta)* species: pregonite slender, apically rounded and covered with tiny spinules (Fig. 89; more curved than in Fig. 100); distiphallus in profile slender, nearly parallel-sided, varied apically (Figs. 122-123); and cerci in posterior view broadened to near tip (Fig. 142; more broadened than in some *S. (Aphantorhapha)* species [Fig. 143], though similar in shape in a very few other *Siphona s.l.* species).

Description

Length: 3.5-4.5mm.

Head (Fig. 13).— Anterior proclinate orbital seta longer than posterior one. Eye of male and female subequal in size, medium to medium-large, 0.76-0.81 head height. Flagellomere 1 of male and female subequal, medium-short to medium length, 0.41-0.52 head height; average width. Aristomere 1 short. Aristomere 2 relatively short, about 1.5X longer than wide. Aristomere 3 long and evenly tapered, pubescent to short plumose. Clypeus narrow and enclosed in membrane to slightly broadened. Palpus short, clavate. Proboscis with prementum medium in length (slightly over half head height in length), labella padlike to moderately lengthened.

Thorax.— Prosternum setulose. Lower katepisternal seta longer than upper anterior seta. Three postsutural dorsocentral setae. Upper part of anepisternum with single setula. Fore tibia with preapical *ad* seta much shorter than *d* seta. Mid tibia with one *ad* seta. Claws short. Wing vein CuA_1 with distal portion 0.35-0.49 length of proximal portion (mean 0.42). Wing setulae: *Sc* ventrally setulose in some specimens; R_1 dorsally distally or entirely setulose, ventrally bare; R_{4+5} setulose from base to beyond *r-m*; CuA_1 bare or setulose.

Abdominal terga 1-5.— Abdomen ovoid in shape. T_{1+2} without median marginal setae, lateral marginal setae absent to weak. T_3-T_5 with average setation.

Male genitalia (Figs. 62, 89, 122-123, 142).— S_5 (Fig. 62) with posterior margins of processes approximately U-shaped; apical lobe distinctly differentiated, apex curved inward in some specimens of *S. singularis* complex; median lobe pointed to narrowly rounded, relatively unmodified; processes moderately setulose. T_6 apparently absent. Ejaculatory apodeme with fan-shaped portion subequal to 2.0X wider than width of hypandrial apodeme. Pregonite (Fig. 89) in profile rather slender and elongate; outer surface short spinose apically, tiny seta posteriorly in *S. singularis* complex, seta absent from single specimen of *S. (A.)* sp. 1. Epiphallus absent. Distiphallus reduced posteriorly, not incised laterally, in profile rather narrow basally, nearly parallel-sided to tip, in *S. singularis* complex with or without (Fig. 122) apical hook anteroventrally, in *S. (A.)* sp. 1 with several hooks radiated from apex ventrally and anteroventrally (Fig. 123). Postgonite rounded apically in *S. singularis* complex, short in *S. (A.)* sp. 1. Surstylus rather short to average length, more or less straight; basally free from epandrium. Cerci average length, in profile rather straight at midlength, in posterior view broadened to near apex (Fig. 142); moderately setose on basal half in *S. (A.)* sp. 1, varied in members of *S. singularis* complex from state in *S. (A.)* sp. 1 to densely setose along length.

Examined male genitalia of: *S. singularis* complex, *S. (A.)* sp. 1.

Female genitalia— Moderately extensible. S_6 bare to sparsely haired posteromedially; slightly keeled posteromedially. T_6 absent; spiracles of segment 6 in membrane dorsal to lateral margins of S_6. S_7 with long anterior apodeme; slightly keeled posteromedially. T_7 absent; (spiracles not located). S_8 much broader than average, haired. T_{10} present as two sclerites.

Examined female genitalia of: *S. singularis*.

Taxonomic changes

Synonymy of S. (Actinocrocuta) chaetosa (Townsend) with S. (Actinocrocuta) singularis (Wiedemann).— The primary types (both male) of *S. chaetosa* (type locality "Trinidad") and *S. singularis* (type locality "Brasilia") are externally very similar, with no significant differences. The male genitalia are less similar, differing particularly in features of the distiphallus and degree of setation on posterior surface of cerci. In the absence of additional material I would be inclined towards retaining both names, but additional material has been examined and includes not only specimens with clearly intermediate states but also specimens with more extreme states. I have not been able to sort these specimens into distinct morphological groups because the apparent differences seem continuous and are not clinally distributed. There is either one very morphologically varied species, or two or more sibling species. Because of the range of observed variation and presence of intermediates, I synonymize the name *S. chaetosa* with *S. singularis*, and refer to this varied taxon as the *S. singularis* complex.

Hosts.   Unknown.

Phylogenetics

Siphona (Actinocrocuta) here comprises the *S. singularis* complex and *S. (Actinocrocuta)* sp. 1. Adults of these taxa are similar in external appearance and coloration (see Recognition section), but these characteristics alone are not good indicators of monophyly because convergence in such features is common among *Siphona s.l.* species. Monophyly of this subgenus is better supported by three characters of the male genitalia: broadened cerci (Fig. 142), slender distiphallus (Figs. 122-123) and slender and apically spined pregonite (Fig. 89). These states are individually present in a few other *Siphona s.l.* species, in species unrelated to one another. The states are therefore homoplastic, though the presence of all three in *S. (Actinocrocuta)* species is better explained by monophyly of the subgenus than by independent development of these states in the two included species. The sister group to *S. (Actinocrocuta)* cannot be established with confidence (it is certainly to be sought among other Neotropical *Siphona s.l.* taxa), so *S. (Actinocrocuta)* is retained as a narrowly defined subgenus of *Siphona s.l.*

Geographic distribution

The *S. singularis* complex is widely distributed throughout the Neotropics, with records from Costa Rica, Colombia, Ecuador, Peru, Brazil (Manaus and southeastern region) and Trinidad. A single male specimen of a new species, referred to above as *S. (A.)* sp. 1, was collected at 400m from Avispas, Madre de Dios, Peru (1-15.X.1962), along with several specimens of the *S. singularis* complex.

List of described species included in *Siphona (Actinocrocuta)*

S   *singularis* (Wiedemann), 1830: 335 *(Tachina)*. Holotype male, Brazil (FSF). Holotype examined.

    syn.   *chaetosa* (Townsend), 1935: 228 (*Actinocrocuta*). Lectotype male (by fixation as "holotype" by Townsend, 1940: 275 [see explanation under "Type designations of Coquillett and Townsend"]), Trinidad (USNM). Lectotype examined. **New synonymy.**

List of examined, undescribed, species included in *Siphona (Actinocrocuta)*

S. (Actinocrocuta) sp. 1: One male from Peru (CNC).

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Siphona (subgenus *Aphantorhapha* Townsend)
Figs. 14, 63, 90, 124, 143.

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Aphantorhapha Townsend, 1919: 586. Type-species, *A. arizonica* Townsend, 1919 (original designation). **New subgeneric status** in *Siphona* Meigen.

Recognition

As presently conceptualized, *S. (Aphantorhapha)* comprises two described and four undescribed New World species, and is one of the more difficult *Siphona* subgenera to diagnose. Adults are rather small (2.0-3.5mm in length) and dark-colored, with more or less average-sized eye and flagellomere 1, three postsutural dorsocentral setae, lower katepisternal seta subequal to or longer than upper anterior seta, crossvein *dm-cu* slightly removed from wing margin, and anal vein extended to wing margin. As these external characteristics are shared by some other species of *Siphona s.l.*, the male genitalia of specimens must be examined for a reliable identification.

One of the two distinctive features of the male genitalia of *S. (Aphantorhapha)* species is the shape of the distiphallus (Fig. 124), which in profile has a characteristically tapered appearance and rounded to pointed tip. The other distinctive feature, though not present in all species (absent from single examined male of *S. atoma* and some specimens of *S. arizonica*), is the slightly broadened cerci (Fig. 143; broadened at midlength rather than to near tip like in *S. (Actinocrocuta)* species, Fig. 142). Like many other *Siphona s.l.* species, the pregonite (Fig. 90) is of average shape, apically bare, and with or without a seta posteriorly.

Description

Length: 2.0-3.5mm.

Head (Fig. 14).— Proclinate orbital setae subequal in length or anterior one longer. Eye of male medium to medium-large, 0.71-0.83 head height; eye of female slightly smaller to slightly larger than in male. Flagellomere 1 of male medium-short to medium length, 0.43-0.54 head height; shape from linear to broadened. Flagellomere 1 of female shorter than in male. Aristomere 1 short. Aristomere two 2.0-4.0X longer than wide. Aristomere 3 long and evenly tapered to short and thickened to near tip, micropubescent to short plumose. Clypeus narrow and enclosed in membrane to slightly broadened. Palpus short, clavate. Proboscis with prementum short to medium in length (about half head height in length), labella padlike in most species, slightly lengthened in *S. (A.)* sp. 2.

Thorax.— Prosternum setulose. Lower katepisternal seta subequal in length or longer than upper anterior seta. Three postsutural dorsocentral setae. Upper part of anepisternum with single setula. Fore tibia with preapical *ad* seta much shorter than *d* seta. Mid tibia with one *ad* seta. Claws short. Wing vein CuA_1 with distal portion 0.44-0.85 length of proximal portion (mean 0.64). Wing setulae: R_1 dorsally bare or entirely setulose, ventrally bare or distally setulose; R_{4+5} setulose to or beyond *r-m*; CuA_1 bare.

Abdominal terga 1-5.— Abdomen ovoid in shape. T_{1+2} without median marginal setae, lateral marginal setae absent to weak. T_3-T_5 with average setation.

Male genitalia (Figs. 63, 90, 124, 143).— S_5 (Fig. 63) with posterior margins of processes slightly obtuse to approximately U-shaped; apical lobe distinctly differentiated, apex curved inward in some species; median lobe rounded to broadly truncate, relatively unmodified; processes moderately setulose. T_6 absent or present as two lateral sclerites or broad dorsally continuous sclerite. Ejaculatory apodeme with fan-shaped portion subequal to 1.5X wider than width of hypandrial apodeme. Pregonite in profile smoothly curved anteriorly (Fig. 90) to rather sharply bent anteriorly at midlength, and more or less pointed apically; posteriorly bare in single specimen of *S. (A.)* sp. 2, with tiny to medium-sized seta in *S. arizonica*, short seta in single examined specimens of *S. atoma* and *S. (A.)* spp. 3 and 4 and medium-sized seta in single examined specimen of *S. (A.)* sp. 1. Epiphallus absent. Distiphallus reduced posteriorly, not incised to slightly incised laterally, with enlarged teeth anterolaterally in *S. arizonica* (Fig. 124) and to lesser extent *S. atoma*, teeth not enlarged beyond size of adjacent spinules in *S. (A.)* spp. 1 to 4, in profile tapered to rounded or pointed tip. Postgonite apically rounded. Surstylus short to rather long and straight; basally free from epandrium. Cerci

in profile short in *S. arizonica* and *S. atoma*, average length in *S. (A.)* spp. 1 to 4; straight to smoothly curved along posterior margin; slightly broadened at midlength in posterior view in some specimens of *S. arizonica* and single dissections of *S. (A.)* spp. 1-4 (Fig. 143), smoothly tapered to tip in some specimens of *S. arizonica* and single dissection of *S. atoma* (similar to Fig. 144); moderately setose on basal half.

Examined male genitalia of: *S. arizonica, S. atoma* and *S. (A.)* spp. 1-4.

Female genitalia.— Short. S_6 with average length hairs. T_6 absent or present as median sclerite; spiracles of segment 6 in membrane dorsal to lateral margins of S_6. S_7 with long anterior apodeme; not keeled posteromedially. T_7 absent or present as small lateral sclerites; spiracles of segment 7 in membrane between segments 6 and 7. S_8 distinctly developed, haired. T_{10} present as two sclerites.

Examined female genitalia of: *S. arizonica*.

Hosts. Unknown.

Phylogenetics

Adults of this subgenus of six species (two described and four undescribed) share a number of external characteristics (see Recognition and Description sections), but none is considered synapotypic of the group.

Monophyly of *S. (Aphantorhapha)* is weakly supported by two slightly derived, but apparently unique, states in the male genitalia. One is the tapered shape of the distiphallus (Fig. 124). The other is the broadened cerci (Fig. 143), which were observed in the single dissections of *S. (A.)* spp. 1-4 and some dissections of *S. arizonica* specimens (*i.e. S. arizonica* with cerci varied from average to broadened). Though the cerci of the single dissected male of *S. atoma* are of average shape, this species is very similar in all other respects to other members of *S. (Aphantorhapha)*. In fact, the short cerci and toothed distiphallus of *S. atoma* suggests it is sister species to *S. arizonica*.

Siphona pulla, described by Reinhard in *Aphantorhapha*, is known only from the female holotype. The type does not agree in all respects with the present concept of *S. (Aphantorhapha)*. and cannot be placed into another supraspecific taxon of *Siphona s.l.* without study of male genitalic characters. *S. pulla* is therefore left as an unplaced species of *Siphona s.l.*

Siphona (Aphantorhapha) is admittedly not very distinctive, and is only recognized as a subgenus because it is apparently monophyletic and because synapotypies between it and other *Siphona s.l.* groups (which would permit a larger and more broadly defined subgenus to be recognized) are unknown.

Geographic distribution

The two described species of *S. (Aphantorhapha)* and *S. (A.)* spp. 3 and 4 are primarily southern Nearctic in distribution. *S. arizonica* is the most widely distributed, ranging from Arizona and western New Mexico through Durango, Chihuahua and Oaxaca to San Cristobal, Chiapas. *S. atoma* is only known from the type series collected from College Station, Texas. *S. (A.)* sp. 3 is known from one male collected from Grant Co., New Mexico, and *S. (A.)* sp. 4 from two males collected near La Ciudad, Durango.

Two new species of *S. (Aphantorhapha)* are recognized from the Neotropics. *Siphona (A.)* sp. 1 is known from a single male collected from Ibarra, in the Imbabura province of Ecuador (2200m, 2-4.VI.1977). The other species, *S. (A.)* sp. 2, is known from several specimens collected over several years from Nova Teutonia, SE Brazil.

List of described species included in *Siphona* (*Aphantorhapha*)

N,S *arizonica* (Townsend), 1919: 586 (*Aphantorhapha*). Holotype male, USA: Arizona, Chiricahua Mtns. (USNM). Holotype examined.

N   *atoma* (Reinhard), 1947: 19 (*Aphantorhapha*). Holotype male, USA: Texas, College Station (CNC). Holotype examined.

List of examined, undescribed, species included in *Siphona* (*Aphantorhapha*)

S. (Aphantorhapha) sp. 1: One male from Ecuador (BMNH).
S. (Aphantorhapha) sp. 2: Three males from SE Brazil (CNC, USP).
S. (Aphantorhapha) sp. 3: One male from New Mexico, USA (JEOH).
S. (Aphantorhapha) sp. 4: Two males from Durango, Mexico (CNC).

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Siphona (subgenus *Aphantorhaphopsis* Townsend)

Figs. 64, 91-92, 125.

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Aphantorhaphopsis Townsend, 1926a: 34. Type-species, *A. orientalis* Townsend, 1926 (original designation). **New subgeneric status** in *Siphona* Meigen.
Asiphona Mesnil, 1954: 9, 10 (as subgenus of *Siphona*). Type-species, *Thryptocera selecta* Pandellé, 1894 (original designation). **New synonym** of *Aphantorhaphopsis* Townsend.

Recognition

This taxon was called *Asiphona* Mesnil previously (*e.g.* Andersen 1983), but *Aphantorhaphopsis* has priority and is used here. It comprises a probably non-monophyletic assemblage of Old World *Siphona s.l.* species not belonging to *Siphona s.s.* or *S. (Ceranthia)* [other *Siphona* subgenera are strictly New World in known distribution]. The rationale for recognizing such an unsatisfactorily-defined group in the formal classification of the Siphonini is explained below in the Phylogenetics section.

Species of *S. (Aphantorhaphopsis)* have a short aristomere 1, lower proepimeral seta undeveloped, lower katepisternal seta at least length of upper anterior one, katepisternum without row of hairs anterior to mid coxa, and anal vein extended to wing margin. These states distinguish *S. (Aphantorhaphopsis)* species from all Old World non-*Siphona s.l.* species.

Siphona s.s. species have a characteristically elongate proboscis, with labella rigid basally and at least as long as the prementum. Most *S. (Aphantorhaphopsis)* species have padlike labella, and are thus easily separated from *Siphona s.s.* species

by this state. The labella of a few *S. (Aphantorhaphopsis)* species are lengthened, and in a very few as long as prementum, but only in Nepal sp. 1 are they also inflexible along basal half (in life) and with reduced number of pseudotracheae as in *Siphona s.s.* species. Nepal sp. 1 is distinguished from *Siphona s.s.* species by its possession of a seta posteriorly on the pregonite (this seta is absent from *Siphona s.s.* species and present in, or absent from, *S. (Aphantorhaphopsis)* species).

  S. (Ceranthia) species are characterized by a cylindrical palpus (Fig. 16), long seta posteriorly on the pregonite (Fig. 94) and distinctive shape of the distiphallus (Fig. 127). Two *S. (Aphantorhaphopsis)* species, Australia sp. 1 and New Guinea sp. 1, have a cylindrical palpus like in *S. (Ceranthia)* species, but these do not have the male genitalic states of that taxon (they have a bare pregonite and the distiphallus is not laterally incised).

Description

Length: 3.0-5.0mm.

  Head.— Anterior proclinate orbital seta subequal to or longer than posterior one. Eye of male medium-small to large, 0.69-0.89 head height; eye of female smaller than or subequal to eye of male. Flagellomere 1 of male short to medium-long, 0.38-0.63 head height; shape linear to broad in most species, subquadrangular in a few. Flagellomere 1 of female subequal or smaller than in male. Aristomere 1 short. Aristomere two 1.5-4X longer than wide. Aristomere 3 long and evenly tapered in most species, short and thickened to near tip in a few; almost bare to short plumose. Clypeus narrow and enclosed in membrane to U-shaped. Palpus short and clavate in most species, long in some species with an elongate proboscis, reduced and cylindrical (as in *S. (Ceranthia)* spp.) in Australia sp. 1 and New Guinea sp. 1. Proboscis with prementum short in most species, slightly lengthened to elongate in a few; labella padlike in most species, slightly lengthened to subequal prementum length in a few with more than basal half flexible in life (*e.g. S. alticola, S. crassulata, S. fera,* Nepal sp. 2 and New Guinea sp. 3), very long and *Siphona*-like (*i.e.* labella inflexible over at least basal half and number of pseudotracheae reduced) in Nepal sp. 1 (proboscis 2.6X head height).

  Thorax.— Prosternum setulose, except bare in Nepal sp. 3. Lower katepisternal seta subequal in length to, or longer than, upper anterior seta. Three or four postsutural dorsocentral setae. Upper part of anepisternum with one setula in most species, two in a few. Fore tibia with preapical *ad* seta much shorter than *d* seta in almost all species, known to be as long as *d* seta only in *S. laticornis.* Mid tibia with one *ad* seta in most species (short in Australia sp. 1), two *ad* setae in Kenya sp. 1 and South Africa sp. 1. Claws short. Wing vein CuA_1 with distal portion 0.26-1.4X length of proximal portion (mean 0.47). Wing setulae: R_1 dorsally bare or distally setulose, ventrally bare in most species, distally setulose in a few; R_{4+5} setulose between base and *r-m* in most species, known to be setulose beyond *r-m* only in Australia sp. 2; CuA_1 bare.

  Abdominal terga 1-5.— Abdomen ovoid in shape. T_{1+2} without median marginal setae, lateral marginal setae absent to strong. T_3-T_5 average or with weak lateral discal setae.

  Male genitalia (Figs. 64, 91-92, 125).— S_5 with posterior margins of processes approximately U-shaped in most species, obtusely angled in a few, almost V-shaped in Nepal sp. 1 (Fig. 64, resembling typical *Actia* shape except median cleft more distinct); apical lobe distinctly differentiated, apex slightly to markedly curved inward in several species; median lobe narrowly to broadly rounded or truncate, relatively unmodified; processes moderately setulose. T_6 varied from two small lateral sclerites to single, narrow to broad, dorsally continuous sclerite. Hypandrial apodeme lengthened in New Guinea sp. 1, very elongate in Nepal sp. 4. Ejaculatory apodeme with fan-shaped portion 0.5-1.5X wider than hypandrial apodeme. Pregonite (Figs. 91-92) in profile curved anteriorly and pointed apically in most species, in others varied from short and broad to long and thin, in *S. nigronitens* expanded basally and fused with hypandrial apodeme, in Kenya sp. 1 expanded ventrolaterally; bare or with small seta posteriorly in most species, large seta present in *S.* nr. *fera* (absent from holotype of *S. fera*). Epiphallus present or absent. Distiphallus (Fig. 125) reduced posteriorly, markedly varied in profile, laterally incised or complete, apically pointed or rounded or truncate, with or without recurved spines along anterior and/or lateral margin, in about half the

species with long posterolateral arm. Postgonite long and pointed in Australia sp. 2, very reduced in *S. nigronitens* and Nepal sp. 4, rounded or truncate in other species. Surstylus markedly varied, short to long, thin to broad, straight to curved posteriorly; basally fused with epandrium in Nepal sp. 4, free from epandrium in other species. Cerci average length and smoothly curved in most species, rather short in a few species, slightly inflexed at midlength in a few species; moderately setose on basal half.

Examined male genitalia of: *S. alticola, S. brunnescens, S. crassulata, S. fera, S.* nr. *fera, S. nigronitens, S. orientalis, S. starkei, S. xanthosoma,* Australia spp. 1-2, Kenya sp. 1, Nepal spp. 1-4, New Guinea spp. 1-3 and Uganda sp. 1. Examined published figure of: *S. siphonoides* (Andersen 1983, fig. 19).

Female genitalia.— Short. S_6 with average length hairs. T_6 absent (not examined in Australia sp. 1 and Nepal sp. 4); spiracles of segment 6 in membrane dorsal to lateral margins of S_6. S_7 with long anterior apodeme; not keeled posteromedially. T_7 absent from most species, present as two small lateral sclerites in Nepal sp. 1; spiracles of segment 7 in membrane between segments 6 and 7. S_8 distinctly developed, haired, broader than average in a few species, large and rather pointed in Australia sp. 1. T_{10} absent from Uganda sp. 1, present as lightly to distinctly sclerotized pair of sclerites or median sclerite in other species.

Examined female genitalia of: Australia sp. 1, Kenya sp. 1, Nepal spp. 1,4, South Africa sp. 1 and Uganda sp. 1. Examined published figure of: *S. samarensis* (Andersen 1983, fig. 5).

Hosts

Known hosts of *S. (Aphantorhaphopsis)* comprise a diverse assemblage of Macrolepidoptera, as might be expected of a grade-based taxon such as this (Table 2). Five host families are represented, of which two, the Noctuidae and Geometridae, are commonly recorded among other siphonines. The three remaining families, the Hesperiidae, Liparidae and Arctiidae, are virtually unreported as hosts of other siphonines (a single record being that of an arctiid host for *Ceromya bicolor*). One European species, *S. samarensis*, is recorded from an economically important pest, the gypsy moth (*Porthetria dispar*), though its level of parasitism is apparently very low.

Given the possibly polyphyletic nature of *S. (Aphantorhaphopsis)* and the meagre extent to which both its species and hosts are known, the diversity of hosts here recorded is probably far from representative for the taxon.

Phylogenetics

The present grouping of Old World species under *S. (Aphantorhaphopsis)* is one of taxonomic convenience, as too little is known about these species to formulate a phylogenetically-based classification. Adults have the derived features of *Siphona s.l.*, and are assignable within the genus to *S. (Aphantorhaphopsis)* by their lack of the apotypic states defining the other *Siphona* subgenera. It is inferred that this group lacks autapotypies because it is composed of several (numerous?) lineages. This taxon is probably either paraphyletic or polyphyletic, depending upon the true relationships of these species with those of other *Siphona* subgenera.

The diverse assemblage of species comprising this group can only be adequately reclassified by a thorough study of at least external and male genitalic characters. Even a revision of described species is apt to be inadequate for both classificatory and identification needs, as many undescribed species are known.

The description above of *S. (Aphantorhaphopsis)* is based upon the study of specimens of as many species as were available. Though this characterization of *S.*

(Aphantorhaphopsis) is recognized as an interim measure until a thorough revision is undertaken, it is nevertheless useful, as it is the first comprehensive review of the included species. Its concept is the same as that of Andersen's (1983) *Asiphona* Mesnil, over which the name *Aphantorhaphopsis* has priority.

Andersen similarly diagnosed this taxon as a group of Old World siphonines belonging to the *Siphona* lineage and lacking the derived states of the other taxa (in his case *Siphona s.s.* and *S. (Ceranthia)* because his revision dealt strictly with Old World siphonines). Andersen found no autapotypies of *Asiphona*, but retained the taxon as a genus and hypothesized a sister group relationship between it and *Ceranthia*. He based this hypothesis on the shared possession in these taxa of a seta on the posterior surface of the pregonite, which is absent from *Siphona s.s.* species. However, the present study has shown that some species of *S. (Aphantorhaphopsis)* lack this seta and many New World *Siphona s.l.* species possess it, so presence of a seta is not synapotypic of this taxon and *S. (Ceranthia)*. The significance of this seta, with respect to the phylogeny of the supraspecific taxa of *Siphona s.l.*, is discussed in the Evolution chapter.

An attempt was made while revising the supraspecific taxa of *Siphona s.l.* to discover species of *S. (Aphantorhaphopsis)* which might have close New World relatives. None was found, perhaps because New World subgenera are mostly Neotropical and southern Nearctic in distribution and are thus likely to be too old to have easily recognized Old World members, if indeed any exist. It was not clearly established whether or not some of the unplaced *Siphona s.l.* species of the northern Nearctic region are closely related to any Old World *S. (Aphantorhaphopsis)* species, though this is a possibility.

Geographic distribution

The 21 described species of *S. (Aphantorhaphopsis)* are fairly evenly distributed throughout the Palearctic, Afrotropical and Oriental regions, with six species described from each of the first two regions and eight from the third. Only one species is described from Australia. Examination of material from the Old World indicates that at least several, perhaps many, undescribed species exist in each region, particularly in the Oriental and Australian regions.

The six described Palearctic species are apparently restricted to Europe (Herting 1984 [species included under broad concept of *Ceranthia*]; no records in publications of Richter) and are keyed and redescribed in Mesnil (1963a-1964: 843-853). Species of the other regions are catalogued in Crosskey (1973, 1976a, 1980), mostly in the genus *Ceromya*. Dear and Crosskey (1982) key three species occurring in the Philippines, *S. angustifrons, S. orientalis* and *S.* nr. *selangor* (all keyed as *Ceromya* species), and species of central Africa and Madagascar are keyed in Mesnil (1954 and 1977b, respectively).

The distribution of *S. (Aphantorhaphopsis)* species cannot be historically interpreted until the phylogenetic relationships among these species are better

known, as well as their relationships with other subgenera of *Siphona*.

List of described species included in *Siphona* (*Aphantorhaphopsis*)

O *alticola* (Mesnil), 1953: 110 (*Crocuta* (*Siphona*)). Holotype male, Burma: Kambaiti (ZMU). Holotype examined. **New combination**.

O *angustifrons* (Malloch), 1930b: 131 (*Actia*). Holotype male, Malaysia: Kedah Peak (BMNH). Holotype examined. **New combination**.

P *brunnescens* (Villeneuve), 1921: 46 (*Actia*). Holotype male, German Democratic Republic: Oberlausitz, Niederoderwitz (CNC). Holotype examined. **New combination**.

O *crassulata* (Mesnil), 1953: 112 (*Crocuta* (*Siphona*)). Holotype male, Burma: Kambaiti (ZMU). Holotype examined. **New combination**.

A *fera* Mesnil, 1954: 26 (described in subgenus *Asiphona*). Holotype male, Zaire: Nyongera (MRAC). Holotype examined. **New combination**.

O *laboriosa* Mesnil, 1957: 48 (described in subgenus *Asiphona*). Holotype male, Burma: Kambaiti (ZMU). Holotype examined. **New combination**.

O *laticornis* (Malloch), 1930b: 131 (*Actia*). Holotype male (not female), Malaysia: Selangor (BMNH). Holotype examined. **New combination**.

O *mallochiana* (Gardner), 1940: 178 (*Actia*). Type(s) puparia, India (?FRI). **New combination**.

    syn.   *perispoliata* (Mesnil), 1953: 108 (*Actia*). Holotype male, China: Canton (BMNH).— Crosskey, 1976a: 213. Holotype examined.

A *nigronitens* Mesnil, 1954: 25 (described in subgenus *Asiphona*). Holotype male, Zaire: Rutshuru (MRAC). Holotype examined. **New combination**.

U *norma* (Malloch), 1929a: 116 (*Actia*). Holotype male, Australia: New South Wales, Como (USNM). Holotype examined. **New combination**.

O *orientalis* (Townsend), 1926a: 35 (*Aphantorhaphopsis*). Holotype male, Indonesia: Sumatra, Fort de Kock (ZMA). Holotype examined.

A *picturata* (Mesnil), 1977b: 179 (*Asiphona*). Holotype male, Madagascar: Belazao (MNHN). **New combination**.

A *pudica* Mesnil, 1954: 27 (described in subgenus *Asiphona*). Holotype male, Zaire: Eala (MRAC). Holotype examined. **New combination**.

P *samarensis* (Villeneuve), 1921: 46 (*Actia*). Holotype female, Russia: Kujbyšev [Samara] (CNC). Holotype examined. **New combination**.

O *selangor* (Malloch), 1930b: 132 (*Actia*). Holotype male, Malaysia: Selangor (BMNH). Holotype examined. **New combination**.

P *selecta* (Pandellé), 1894: 112 (*Thryptocera*). Syntypes, France: Var, Hyères (MNHN). **New combination**.

P *siphonoides* (Strobl), 1898: 235 (*Gymnopareia*). Holotype male, Austria: Steiermark, Gesäuse (NMBA). **New combination**.

    syn.   *brunneipalpis* (Villeneuve), 1921: 45 (*Actia*). Holotype male, Federal

Republic of Germany: Harz (CNC).— Mesnil, 1963a: 848. Holotype examined.

A   *speciosa* Mesnil, 1954: 28 (described in subgenus *Asiphona*). Holotype male, Zaire: Rutshuru (MRAC). Holotype examined. **New combination**.

P   *starkei* (Mesnil), 1952b: 155 (*Actia*). Holotype male, German Democratic Republic: nr. Bautzen, Hennerstadt (CNC). Holotype examined. **New combination**.

P   *verralli* (Wainwright), 1928: 208 (*Actia*). Holotype male, Scotland: Sutherlandshire, Mound (HDE). Holotype examined. **New combination**.

A   *xanthosoma* Mesnil, 1954: 28 (described in subgenus *Asiphona*). Holotype male, Zaire: Rwindi (MRAC). Holotype examined. **New combination**.

List of examined, undescribed, species included in *Siphona* (*Aphantorhaphopsis*)

S. (Aphantorhaphopsis) Australia sp. 1: One male, three females from Queensland (DPI).

S. (Aphantorhaphopsis) Australia sp. 2: One male from Karumba, Queensland (DPI).

S. (Aphantorhaphopsis) Kenya sp. 1: One male and several females from Kenya (CAS, USNM).

S. (Aphantorhaphopsis) Nepal sp. 1: Males and one female from Nepal (CNC).

S. (Aphantorhaphopsis) Nepal sp. 2: One male, one female from Kathmandu (CNC).

S. (Aphantorhaphopsis) Nepal sp. 3: Two males from Nepal (CNC).

S. (Aphantorhaphopsis) Nepal sp. 4: One male, one female from Nepal (CNC).

S. (Aphantorhaphopsis) New Guinea sp. 1: Males and one female from New Guinea (BPBM).

S. (Aphantorhaphopsis) New Guinea sp. 2: Three males from ne. Mur Mur P. (BPBM).

S. (Aphantorhaphopsis) New Guinea sp. 3: One male from se. Mt. Saint Mary (BPBM).

S. (Aphantorhaphopsis) South Africa sp. 1: Two females from Cape Good Hope Nat. Res. (USNM).

S. (Aphantorhaphopsis) Uganda sp. 1: Males and females from Uganda, one female from Rhodesia (CNC, USNM).

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Siphona (subgenus *Baeomyia* O'Hara)

Figs. 15, 22, 38, 93, 126.

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Baeomyia O'Hara, 1984: 1390. Type-species, *Aphantorhapha hurdi* Reinhard, 1959 (original designation). **New subgeneric status** in *Siphona* Meigen.

Recognition

Adults of *S. (Baeomyia)* species are among the smallest of siphonines, measuring 2-3mm in length. They are only recorded from western North America and are easily recognized among New World siphonines by the absence of an *ad* seta on the mid tibia (Fig. 38) - a state only shared with several Old World *Actia* and *Ceromya* *s.s.* species. Also diagnostic is the elongate aristomere 1, which is subequal in length to aristomere 2 (Fig. 15; only as long in a few Old World siphonines). *S. (Baeomyia)* species are also characterized by padlike labella, three postsutural dorsocentral setae, wing vein R_{4+5} not setulose beyond crossvein *r-m*, anal vein extended to wing margin, and crossvein *dm-cu* far removed from wing margin (Fig. 22).

Description

Length: 2.0-3.0mm.

Head (Fig. 15; also see head profiles in O'Hara 1984, figs. 1-5.).— Anterior proclinate orbital seta subequal in length to posterior one. Eye of male and female subequal, small to medium-large, 0.65-0.83 head height. Flagellomere 1 of male short to medium length, 0.39-0.56 head height; shape average to broadly subquadrangular. Flagellomere 1 of female smaller than in male or subequal in size. Aristomere 1 elongate, subequal in length to aristomere 2, each 2.4-4.6X longer than wide. Aristomere 3 almost bare, very short, evenly tapered or thickened to near tip. Clypeus U-shaped. Palpus short, clavate. Proboscis with prementum short, labella padlike.

Thorax (Fig. 22).— Prosternum bare or sparsely setulose. Lower katepisternal seta shorter than or subequal in length to upper anterior seta. Three postsutural dorsocentral setae. Upper part of anepisternum with single setula. Fore tibia with preapical *ad* seta much shorter than *d* seta. Mid tibia lacking *ad* seta. Claws short. Wing (Fig. 22 and O'Hara 1984, fig. 10): CuA_1 with distal portion 0.64-1X length of proximal portion (*i.e. dm-cu* far removed from wing margin; mean 0.85). Wing setulae: R_1 dorsally bare or with one setula apically on bend, ventrally bare; R_{4+5} setulose between base and *r-m*; CuA_1 bare.

Abdominal terga 1-5.— Abdomen ovoid in shape. T_{1+2} without median or lateral marginal setae. T_3-T_5 with average setation, setae weakly to strongly developed.

Male genitalia (Figs. 93, 126 and O'Hara 1984, figs. 6-9).— S_5 with posterior margins of processes approximately U-shaped; apical lobe distinctly differentiated; median lobe rounded, relatively unmodified; processes sparsely to moderately setulose. T_6 narrow to broad, dorsally continuous. Ejaculatory apodeme with fan-shaped portion 1.0-1.5X wider than hypandrial apodeme. Pregonite (Fig. 93) in profile curved anteriorly, pointed apically; with tiny seta posteriorly (not shown in O'Hara 1984). Epiphallus absent. Distiphallus (Fig. 126) reduced posteriorly, not incised laterally, without enlarged teeth anteriorly or ventrally, in profile apically truncate. Postgonite short to average in size, apically rounded. Surstylus almost straight to sharply curved posteriorly; basally free from epandrium. Cerci short to average length, smoothly curved (O'Hara 1984, figs. 7-9) or sharply inflexed at midlength (O'Hara 1984, fig. 6); moderately setose on basal half.

Examined male genitalia of: *S. hurdi, S. juniperi, S. sonorensis* and *S. xanthogaster* (all shown in O'Hara 1984, figs. 6-9).

Female genitalia.— Short. S_6 with average length hairs. T_6 absent; spiracles of segment 6 in membrane dorsal to lateral margins of S_6. S_7 with long anterior apodeme; not keeled posteromedially. T_7 absent; spiracles of segment 7 in membrane between segments 6 and 7. S_8 distinctly developed, haired. T_{10} absent.

Examined female genitalia of: *S. antennata, S. hurdi, S. sonorensis* and *S. xanthogaster* (all shown in O'Hara 1984, figs. 11-14 [fig. 14, *S. antennata*, mislabelled as *B. juniperi*]).

Hosts

Hosts of two *S. (Baeomyia)* species are known, and are larvae belonging to the geometrid genus *Semiothisa* (Table 2 and O'Hara 1984).

Phylogenetics

S. (Baeomyia) is a monophyletic taxon based on several synapotypies (see O'Hara 1984: 1388-1389). These include absence of an *ad* seta on the mid tibia (this seta independently lost in a few Old World *Actia* and *Ceromya s.s.* species), aristomere 1 subequal in length to aristomere 2 (a rare state present in a few, unrelated, Old World siphonines), very small-sized adults, very short aristomere 3 (figs. 1-5 in O'Hara 1984), and crossvein *dm-cu* far removed from wing margin (Fig. 22). The last state is possibly not autapotypic of *S. (Baeomyia)* because it is shared with some other *Siphona s.l.* species (see Table 1); the position of *dm-cu* is such a labile character among siphonines that it is difficult to establish among which lineages its derived state (*i.e.* far removed from wing margin) is synapotypic, and

among which it is convergent (O'Hara 1984: 1388).

Geographic distribution

S. (Baeomyia) species are restricted in distribution to western North America. Known distributions are shown and discussed in O'Hara (1984).

List of described species included in *Siphona* (*Baeomyia*)

N   *antennata* (O'Hara), 1984: 1393 (*Baeomyia*). Holotype male, USA: Arizona, Graham Co., near Marijilda canyon (CAS). Holotype examined.

N   *hurdi* (Reinhard), 1959: 161 (*Aphantorhapha*). Holotype male, USA: California, Panamint Mtns. (CAS). Holotype examined.

N   *juniperi* (O'Hara), 1984: 1395 (*Baeomyia*). Holotype male, Canada: British Columbia, Williams Lake (CNC). Holotype examined.

N   *sonorensis* (O'Hara), 1984: 1393 (*Baeomyia*). Holotype male, USA: Arizona, Graham Co., 2.4km. west on Hwy. 366 from Hwy. 666 (CNC). Holotype examined.

N   *xanthogaster* (O'Hara), 1984: 1394 (*Baeomyia*). Holotype male, Canada: British Columbia, Vermilion (CNC). Holotype examined.

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Siphona (subgenus *Ceranthia* Robineau-Desvoidy)
Figs. 16, 44, 46, 65, 94, 127.

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Ceranthia Robineau-Desvoidy, 1830: 88. Type-species, *C. fulvipes* Robineau-Desvoidy, 1830 (by designation of Robineau-Desvoidy, 1863: 685) = *Ceromya abdominalis* Robineau-Desvoidy, 1830. **New subgeneric status** in *Siphona* Meigen.

Recognition

Members of this subgenus are widely distributed, and with few exceptions are easily recognized. Adults are characterized externally by a cylindrical palpus (Fig. 16), a derived state within the Siphonini. This state is also present in *S. (Aphantorhaphopsis)* Australia sp. 1 and New Guinea sp. 1, but these species do not have *S. (Ceranthia)*-like male genitalia (see below), and seem more closely related to certain species of *S. (Aphantorhaphopsis)*.

Two derived features of the male genitalia are also characteristic of *S. (Ceranthia)* species. The posterolateral margins of the distiphallus are incised to varied degrees, with distinct posterolateral arm (one per side; Fig. 127). In addition, a seta projects posteriorly from the pregonite (Fig. 94), and is larger than in all but a very few other *Siphona* species. Atypical in this respect is *S. (Ceranthia)* Mauritius sp. 1, in which this seta is absent. This species possesses a cylindrical palpus and *S. (Ceranthia)*-like distiphallus, and is recognized as a member of this subgenus by these features.

Adult females of *S. (Ceranthia)* species have a posteromedially keeled (Figs. 44, 46) sternum 7, and though this state is not unique to species of this subgenus, it is apparently universal among its members.

Description

Length: 3.0-5.5mm.

Head (Fig. 16).— Anterior proclinate orbital seta subequal in length to posterior one in most species. Eye of male medium-small to large, 0.69-0.88 head height; eye of female usually smaller than in male. Flagellomere 1 of male medium-short to medium-long, 0.42-0.66 head height; shape broad to subquadrangular. Flagellomere 1 of female shorter and narrower than in male. Aristomere 1 short. Aristomere two 2.0-8.0X longer than wide, generally less than 4X. Aristomere 3 almost bare to micropubescent, rather short and evenly tapered. Clypeus varied from narrow and enclosed in membrane to U-shaped. Palpus short or reduced, cylindrical (not apically clavate). Proboscis with prementum short, labella padlike.

Thorax.— Prosternum setulose. Lower katepisternal seta longer than upper anterior seta. Three or four postsutural dorsocentral setae. Upper part of anepisternum with single setula in most species, with two in a few. Fore tibia with preapical *ad* seta much shorter than *d* seta. Mid tibia with one *ad* seta. Claws short. Wing vein CuA_1 with distal portion 0.30-0.51 length of proximal portion (*i.e.* *dm-cu* near wing margin; mean 0.42). Wing setulae: R_1 bare dorsally and ventrally in most species, distally setulose dorsally in a few, distally setulose dorsally and ventrally in *S. terrosa*; R_{4+5} setulose between base and *r-m* in most species, beyond *r-m* in *S. pallida*; CuA_1 bare.

Abdominal terga 1-5.— Abdomen ovoid in shape. T_{1+2} without median marginal setae; lateral marginal setae strong. T_3-T_5 average in most species, with extra pair of lateral marginal setae on T_3 in a few species.

Male genitalia (Figs. 65, 94, 127).— S_5 (Fig. 65) little varied; posterior margins of processes approximately U-shaped; apical lobe large and distinctly differentiated, in most species apex curved inward; median lobe rounded, relatively unmodified; processes sparsely to moderately setulose. T_6 narrow to broad, dorsally continuous or narrowly discontinuous. Ejaculatory apodeme with fan-shaped portion 1.0-1.5X wider than hypandrial apodeme. Pregonite (Fig. 94) in profile curved anteriorly, more or less pointed apically; large seta posteriorly (except bare in Mauritius sp. 1). Epiphallus absent. Distiphallus (Fig. 127) reduced posteriorly, laterally incised to form posterolateral arm extended slightly to markedly beyond anterior margin; anterior margin spinulose or toothed. Postgonite apically rounded or truncate. Surstylus straight, extended slightly beyond tip of cerci; basally free from epandrium. Cerci average length, smoothly curved at midlength; moderately setose on basal half.

Examined male genitalia of: *S. abdominalis* (fig. 20 in Andersen 1983, as *Ceranthia fulvipes*), *S. flavipes*, *S. plorans*, *S. scutellata*, Ethiopia sp. 1, Mauritius sp. 1 and U.S. spp. 1-5.

Female genitalia (Figs. 44, 46).— Short to elongate (*e.g.* U.S. sp. 7). S_6 with average length hairs, ventrally flat or slightly keeled posteromedially. T_6 absent; spiracles of segment 6 in membrane dorsal to lateral, or anterolateral, margins of S_6. S_7 with long anterior apodeme; distinctly keeled posteromedially, in a few species posterior margin narrow and elongate and covering S_8. T_7 absent; spiracles of segment 7 in membrane dorsal to anterolateral margins of S_7. S_8 distinctly developed, haired. T_{10} present as two sclerites.

Examined female genitalia of: *S. abdominalis*, *S. flavipes* and U.S. spp. 1-7. Examined published figure of: *S. tenuipalpis* (Andersen 1983, fig. 6).

Hosts

The hosts of four *S. (Ceranthia)* species are known, and these all belong to the Geometridae (Table 2).

Phylogenetics

S. (Ceranthia) is a clearly defined, monophyletic lineage of *Siphona s.l.* The cylindrical palpus of adults (Fig. 16) has long been recognized as the distinguishing feature (and synapotypy) of this group, and to this are added two genitalic states

which further support monophyly of the subgenus: the distiphallus is characteristically incised posterolaterally, with distinct posterolateral projection (Figs. 127), and the pregonite possesses a large seta posteriorly (Fig. 94). Females possess a posteromedially keeled (Figs. 44, 46) sternum 7, and larvae (so far as known) are parasitic only on larval geometrids, but these characteristics may not be autapotypic of *S. (Ceranthia)* species.

Two species assigned to *S. (Aphantorhaphopsis)* also have a cylindrical palpus - Australia sp. 1 and New Guinea sp. 1. These species do not possess other derived states of *S. (Ceranthia)*, and seem to have developed a cylindrical palpus independently of *S. (Ceranthia)* species. Other characters suggest that they are closely related to species with a normal palpus belonging to the broadly defined *S. (Aphantorhaphopsis)*. With exclusion of these species from *S. (Ceranthia)*, no species of this subgenus are known from the Australian region.

S. (Ceranthia) Mauritius sp. 1 has the derived states of the palpus and distiphallus found in other *S. (Ceranthia)* species, but lacks the large seta on the pregonite which is present in other known species of this taxon. I hypothesize that this seta was present in the groundplan of *S. (Ceranthia)* because at least a small seta is widely distributed among other *Siphona* lineages (Table 1). Therefore lack of this seta from Mauritius sp. 1 is interpreted as a secondary loss.

Geographic distribution

Eight described *S. (Ceranthia)* species are in the Palearctic region, five in the Afrotropical region and one in the Nearctic region. Five of the eight Palearctic species are apparently very limited in distribution, with one each in England (*S. lichtwardtiana*), northern France (*S. tristella*) and Algeria (*S. jocosa*), and two in Japan (*S. japonica* and *S. sulfurea*). More widespread are *S. abdominalis* (common throughout Europe and collected from Mongolia and Chita region (Herting 1973 [as "*Ceranthia* sp. aff. *anomala* Zett." - perhaps a new species], Richter 1975, 1980), *S. tenuipalpis* (described from Berlin, and Zlatoust in the Ural Mtns.) and *S. pallida* (described from Austria, and if correctly identified then also found on the Kuril Islands (Richter 1976b)). A key to the described Palearctic species of *S. (Ceranthia)* is presented in Mesnil (1975: 1399-1400), and distributions are summarized in Herting 1984 (with species of *S. (Aphantorhaphopsis)* included in *Ceranthia*). I have seen specimens of a new Palearctic species from Ethiopia.

Known ranges of the five described Afrotropical *S. (Ceranthia)* species are given in Crosskey (1980). All were described by Mesnil, and their distributions reflect his work on the fauna of the upper Congo area (four species) and Madagascar (one species). I suspect that the *S. (Ceranthia)* fauna of the Afrotropical region is much more diverse than presently recognized.

There are no described *S. (Ceranthia)* species in the Oriental and Australian regions. I have not seen any specimens of *S. (Ceranthia)* species among borrowed Australian siphonines, but examined one female belonging to the subgenus from

Coimbatore in southern India (CNC specimen).

The New World *S. (Ceranthia)* are very inadequately known. The single described species, *S. flavipes*, is recorded from eastern Canada and northeastern USA. Approximately six undescribed *S. (Ceranthia)* species occur in North America, and are mostly eastern or western in distribution. The most southern record for *S. (Ceranthia)* in the New World is southwestern New Mexico, USA.

List of described species included in *Siphona* (*Ceranthia*)

P *abdominalis* (Robineau-Desvoidy), 1830: 87. (*Ceromya*). Type(s), France (lost).

   syn.   *fulvipes* (Robineau-Desvoidy), 1830: 88 (*Ceranthia*). Holotype male, France: Saint Sauveur (lost).— Herting, 1974: 18.

           microcera (Robineau-Desvoidy), 1830: 88 (*Ceromya*). Type(s), France: near Paris (lost).— Mesnil, 1963a: 840.

           anomala Zetterstedt, 1849: 3213, 3221. Two syntypes, Denmark (UZI).— Herting, 1974: 18.

           vivida (Robineau-Desvoidy), 1850: 196 (*Ceromya*). Types, France: near Paris (lost).— Herting, 1974: 18.

           grisea (Robineau-Desvoidy), 1850: 198 (*Ceromya*). Type(s) male, France: near Paris (lost).— Bezzi and Stein, 1907: 389.

           flavipes (Robineau-Desvoidy), 1850: 200 (*Ceranthia*). Unjustified emendation of *C. fulvipes* Robineau-Desvoidy, 1830.

N *flavipes* (Coquillett), 1897: 58 (*Thryptocera*). Holotype female, USA: New Hampshire, White Mtns. (USNM). Holotype examined.

P *japonica* (Mesnil), 1963b: 33 (*Ceranthia*). Holotype male, Japan: Kyushu (CNC). Holotype examined.

P *jocosa* (Villeneuve), 1942b: 134 (*Actia*). Holotype male, Algeria: Algiers (CNC). Holotype examined.

A *lacrymans* (Mesnil), 1954: 24 (*Ceranthia*). Holotype male, Zaire: Karisimbi (MRAC). Holotype examined.

P *lichtwardtiana* (Villeneuve), 1931: 61 (as variety of *Actia anomala* (Zetterstedt)). Type, locality not given (ZMHU; not located, possibly lost).

A *livoricolor* (Mesnil), 1977b: 178 (*Ceranthia*). Holotype female, Madagascar: Anjavidilava (MNHN).

P *pallida* (Herting), 1959: 423 (*Ceranthia* (*Actia*)). Holotype female, Austria: Aflenz, Dorfmeister (NMV). Holotype examined.

A *plorans* (Mesnil), 1954: 24 (*Ceranthia*). Holotype male, Rwanda: Sabinyo (MRAC). Holotype examined.

A *scutellata* (Mesnil), 1954: 22 (*Ceranthia*). Holotype male, Zaire: Rweru (MRAC). Holotype examined.

P *sulfurea* (Mesnil), 1971: 72 (*Ceranthia*). Holotype female, Japan: Hokkaido,

Nukabira (CNC).

P   *tenuipalpis* (Villeneuve), 1921: 46 (*Actia*). Two male syntypes: Berlin, Federal Republic of Germany and Zlatoust, USSR (CNC). Syntypes examined.

A   *terrosa* (Mesnil), 1954: 23 (*Ceranthia*). Holotype male, Rwanda: Kundhuru (MRAC). Holotype examined.

P   *tristella* (Herting), 1966: 5 (*Ceranthia*). Holotype male, Switzerland: Wallis, Tanay (ETH). Holotype examined.

List of examined, undescribed, species included in *Siphona* (*Ceranthia*)

S. (Ceranthia) Ethiopia sp. 1: One male from Addis Abbaba (AMNH).

S. (Ceranthia) Mauritius sp. 1: Two males from Les Mares (CNC).

S. (Ceranthia) U.S. sp. 1: One male, females ranging from Washington state to California, USA (PHA, WSUP).

S. (Ceranthia) U.S. sp. 2: Two males, females from northeastern North America (CAS, CNC, MSU).

S. (Ceranthia) U.S. sp. 3: One male, one female from New Mexico, USA (JEOH).

S. (Ceranthia) U.S. sp. 4: Males and females from northeastern North America (CNC, PHA, USNM, WLD, WSUP).

S. (Ceranthia) U.S. sp. 5: Males and females from California, USA (CAS, JEOH, PHA, USNM).

S. (Ceranthia) U.S. sp. 6: Two females from British Columbia, Canada (CAS, CNC).

S. (Ceranthia) U.S. sp. 7: One female from Nevada, USA (USNM).

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Siphona (subgenus *Pseudosiphona* Townsend)

Figs. 17, 66, 95, 128, 140, 162.

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Pseudosiphona Townsend, 1916: 622. Type-species, *Siphona brevirostris* Coquillett, 1897 (original designation). **New subgeneric status** in *Siphona* Meigen.

Recognition

This taxon is one of the more diverse subgenera of New World *Siphona s.l.*, despite the fact that only its type species, *S. brevirostris*, is described. It comprises two species north of Mexico and approximately 18 south of the United States.

Adults of most *S. (Pseudosiphona)* species have a characteristic habitus, distinctive male genitalia, and unique larval cephalopharyngeal skeleton. However, interspecific variation is common and certain species depart from the average condition in one or more states. Because variation from the typical features is particularly prevalent among external characters, and some other *Siphona s.l.* species appear externally similar, examination of male genitalia is essential for the recognition of members of this subgenus. The following diagnosis includes a suite of characteristics shared by most species of *S. (Pseudosiphona)*, though some species deviate from it in one or more states: adults are light colored with mostly yellow legs, light brown thoracic dorsum, and generally heavy pruinosity on the anterior fourth of abdominal terga and very sparse pruinosity over rest of abdomen (in contrast to the more evenly pruinose abdomens of most other New World *Siphona s.l.* species). Head features are markedly varied, but the following

combination of states is common to most *S. (Pseudosiphona)* species (Fig. 17): row of short hairs extended from parafrontal to halfway down parafacial, medium-sized flagellomere 1, arista distinctly haired, eye medium-large, and proboscis with labella slightly more than half length of prementum.

S. (Siphonopsis) is a very diverse Neotropical taxon and its members can generally be distinguished externally from those of *S. (Pseudosiphona)* by their more pruinose abdomen, shorter row of parafacial hairs, almost bare arista and slightly longer labella. Some members of these taxa are rather similar despite these differences between most species, but features of the male genitalia reliably separate them.

S. (Pseudosiphona) sp. 15 is the least typical of the subgenus in head characteristics, having an elongate prementum and labella like in *Siphona s.s.* species. The male genitalia of this species deviate slightly from the average condition (described below; not resembling the male genitalia of *S. (Siphona)* species), but features of the first instar confirm its placement here.

The male genitalia of most *S. (Pseudosiphona)* species are very distinctive. In most species the pregonite (Fig. 95) is broadened, anterolaterally spinulose, and has one to several tiny setae posteriorly; possession of all three of these states is apparently unique to *S. (Pseudosiphona)*. In a few species the pregonite is more J-shaped. Spinules are present in all examined specimens, but this state is shared with other taxa (though these other taxa have a more slender pregonite). The possession of more than one posterior seta on the pregonite is apparently unique to *S. (Pseudosiphona)* species, though at least one species has only one seta as in some other *Siphona s.l.* species.

The distiphallus of most *S. (Pseudosiphona)* species is unusually uniform in shape (Fig. 128). It is triangular and apically pointed in profile and anterolaterally spined in all but a very few species, and this shape is unique to *S. (Pseudosiphona)*. Few species have an apically truncate distiphallus, but these have the typical states of the pregonite.

The cerci of most *S. (Pseudosiphona)* species are sharply inflexed at midpoint (Fig. 140). This state can be seen during external examination of most males and is not present in many other New World *Siphona s.l.* species (see Table 1). This state is not diagnostic of *S. (Pseudosiphona)* since some of its species have smoothly curved cerci.

S. (Pseudosiphona) sp. 15, mentioned above as having a *Siphona s.s.* head habitus, is easily recognized as a *S. (Pseudosiphona)* species by its male genitalia. The pregonite is J-shaped rather than broadened, but has two tiny setae posteriorly as in most other *S. (Pseudosiphona)* species. The distiphallus is of the typical *S. (Pseudosiphona)* shape, though the cerci are smoothly curved in profile.

The cephalopharyngeal skeleton of first instars provides one of the best character states by which to recognize *S. (Pseudosiphona)* species, though is not likely to be routinely examined. The labrum is elongate and hook-like in most (but not all)

species (Fig. 162), and this state is unique to *S. (Pseudosiphona)* species among *Siphona s.l.* species (see O'Hara in press "a").

Description

Length: 2.0-5.0mm.

Head (Fig. 17).— Proclinate orbital setae subequal in length or anterior one longer. Eye of male medium to large, 0.73-0.86 head height; eye of female slightly smaller to slightly larger than in male. Flagellomere 1 of male short to medium-short, 0.38-0.48 head height; shape rather linear in most species, average to subquadrangular in a few. Flagellomere 1 of female subequal or smaller than in male. Aristomere 1 short in most species, as long as wide in at least one species. Aristomere 2 relatively short, 1.5-2X longer than wide. Aristomere 3 short to long and evenly tapered, micropubescent to medium plumose. Clypeus narrow to slightly broadened, enclosed in membrane. Palpus short, clavate. Proboscis with prementum short to elongate (up to head height in length), between 0.5-0.7 head height in most species, labella slightly to moderately lengthened, in most species between 0.6-0.7 prementum length, quite elongate (0.8-1.0 prementum length) with basal half flexible or inflexible in life (latter state *Siphona*-like) in a few species.

Thorax.— Prosternum setulose. Lower katepisternal seta subequal in length or longer than upper anterior seta. Three postsutural dorsocentral setae. Upper part of anepisternum with one or two setulae. Fore tibia with preapical *ad* seta much shorter than *d* seta. Mid tibia with one *ad* seta. Claws short. Wing vein CuA_1 with distal portion 0.36-0.74 length of proximal portion (mean 0.60). Wing setulae: R_1 dorsally bare, or distally or entirely setulose, ventrally bare. R_{4+5} setulose to or beyond *r-m*; CuA_1 bare.

Abdominal terga 1-5.— Abdomen ovoid in shape. T_{1+2} without median marginal setae, lateral marginal setae absent from most species, weakly developed in a few. T_3-T_5 with average setation.

Male genitalia (Figs. 66, 95, 128, 140).— S_5 (Fig. 66) with posterior margins of processes approximately U-shaped (except almost V-shaped in *S. (P.)* sp. 11, and resembling typical *Actia* shape except median cleft more distinct); apical lobe distinctly differentiated in most species, rather short in *S. (P.)* sp. 19, apex curved inward in a few species; median lobe broadly rounded to truncate and relatively unmodified in most species, with accessory lobe slightly developed in a few species; processes moderately setulose. T_6 absent or present as two lateral sclerites. Ejaculatory apodeme with fan-shaped portion subequal in width to width of hypandrial apodeme. Pregonite in profile broad along most of length and apically rounded or pointed in most species (Fig. 95), rather J-shaped in a few; outer surface short spinose on apical half or less and one to several (in most species several) tiny setae posteriorly. Epiphallus absent. Distiphallus (Fig. 128) reduced posteriorly, not incised laterally, with enlarged spines anterolaterally in almost all species, in profile triangular and apically pointed in most species, subquadrangular and apically truncate in *S. (P.)* spp. 18 and 19, deeply incised anteriorly in most species. Postgonite apically rounded. Surstylus (Fig. 140) varied from average length to elongate, narrow to broad, in most species straight, in a few curved posteriorly; basally free from epandrium. Cerci varied from short to elongate, in profile average width to thick and smoothly curved (a few species) to sharply inflexed at midlength (most species, Fig. 140); moderately (most species, Fig. 140) to densely (a few species) setose on basal half.

Examined male genitalia of: *S. brevirostris, S. (P.)* spp. 1-13,15,17-19.

Female genitalia.— Short to moderately extensible. S_6 with short to long hairs apically, ventrally flat in most species, slightly keeled posteromedially in *S. (P.)* sp. 15, sharply keeled posteromedially in *S. (P.)* sp. 17. T_6 absent; spiracles of segment 6 in membrane dorsal to lateral margins of S_6. S_7 with anterior apodeme rather short in *S. (P.)* sp. 17, long in other species; flat or slightly to markedly keeled posteromedially, average length to elongate, in *S. (P.)* sp. 1 elongate and posteromedially pointed and keeled. T_7 absent or present as two tiny to small lateral sclerites; spiracles of segment 7 in membrane between segments 6 and 7 in most species, in membrane dorsal to posterior margin of S_6 in *S. (P.)* sp. 17. S_8 distinctly developed, almost bare in *S. (P.)* sp. 3, with thick setae in *S. (P.)* sp. 17, average setation in other species. T_{10} present as median sclerite or paired sclerites.

Examined female genitalia of: *S. (P.)* spp. 1-4,14-17.

Taxonomic changes

Lectotype designation for Siphona brevirostris Coquillett.— *Siphona (Pseudosiphona) brevirostris* was described in *Siphona s.s.* by Coquillett in his

"Revision of the Tachinidae" (1897: 76). In that work Coquillett routinely published USNM type numbers for his new species and appropriately labelled his holotypes in the collection (see general discussion of Coquillett's type designations near the beginning of the Classification chapter). Coquillett's type series of *S. brevirostris* consists of three specimens (two females and one male - not three females as published), two of which (both females) were attached to the same pin. The pin with the male specimen bears a paratype label and the other pin, with the two females, bears a type label and a handprinted Townsend label: "Pseudosiphona brevirostris Coq. Gnt. mss." [Gnt. = Genotype, referring to Townsend's selection of *S. brevirostris* as type species of *Pseudosiphona* Tnsd.]. It is evident that both Coquillett and Townsend intended one of the females on the double-mounted pin to be the holotype of *S. brevirostris*, but it is not clear which one. It seems appropriate to consider all three specimens as syntypes, and to select one of the females as lectotype. Accordingly, the two female specimens have been removed to separate pins and one selected, and here designated, lectotype of *Siphona brevirostris* Coquillett. A red bordered label has been attached to the pin bearing the lectotype, and reads: "LECTOTYPE/ Siphona/ brevirostris Coq./ O'Hara designation" (the diagonal slashes indicate separate lines on label). The lectotype also bears the following labels: (1) From Miss/ Murtfeldt, (2) 6, (3) Type/ No. 3574/ U.S.N.M. [red USNM label], (4) Siphona/ brevirostris/ Coq. [Coquillett's handprinted label], (5) Pseudosiphona/ brevirostris Coq./ Gnt. mss. [Townsend's handprinted label]. The lectotype is pinned with a minuten dorso-ventrally through the thorax, and is in good condition except for loss of the right mid leg and tarsi of the left mid and hind legs. The remaining two specimens of the type series, a male and female, are labelled as paralectotypes.

Hosts

Two new host records are known for *S. (Pseudosiphona)*, based on label data accompanying adult specimens in the USNM: one from caterpillars of a lycaenid butterfly (collected in Costa Rica), and the other from larvae of *Chloropteryx* sp. (collected in Trinidad) (Table 2).

Arnaud (1978) records *Siphona brevirostris* from *Oidaematophorus homodactylus* (Table 2), citing the work of Schaffner (1959). This record is probably in error because specimens of *S. brevirostris* are extremely scarce in collections, and their proper identification is very difficult (so few identified specimens are known that comparison with type specimens is almost essential for reliable determination - see discussion concerning the geographic distribution of *S. brevirostris* below).

Phylogenetics

Most *S. (Pseudosiphona)* species have a characteristic habitus (see Recognition section), but some species deviate from it and a few other *Siphona s.l.* species

approximate it, so no external synapotypies of *S. (Pseudosiphona)* are proposed here. Other character states, in the male genitalia and first instar, provide better evidence for monophyly of this group.

Two structures of the male genitalia, the pregonite and distiphallus, have states unique to *S. (Pseudosiphona)* species. Three characters are recognized on the pregonite: shape, presence or absence of spinules anterolaterally, and presence or absence of a seta(e) posteriorly. Though spinules are on the pregonite of all examined *S. (Pseudosiphona)* species, their presence in some other New World *Siphona s.l.* species indicates this state is not unique to this subgenus. States for the other two characters are unique to *S. (Pseudosiphona)* and are interpreted as synapotypies. The first is the characteristically broadened shape of the pregonite, and the second is the presence of more than one seta posteriorly. A few *S. (Pseudosiphona)* species lack one or the other of these states, but not both. A triangular and anterolaterally spined distiphallus (Fig. 128) is hypothesized as another synapotypy of *S. (Pseudosiphona)* species. The few species which depart from this shape are interpreted as derived for this character as they have the derived states of the pregonite.

First instars of five of the seven examined *S. (Pseudosiphona)* species have an elongate, hook-like, labrum (Fig. 162). This state is interpreted as apotypic because other *Siphona s.l.* species have a hatchet-like labrum. Two species of *S. (Pseudosiphona)* have a slightly broadened labrum (in dorsal-ventral plane), but this state is considered secondarily (and independently) derived in these species for reasons given in O'Hara (in prep.).

Geographic distribution

Siphona (Pseudosiphona) is primarily a Neotropical group, for which I am aware of only two species north of Mexico: *S. brevirostris* and undescribed species *S. (P.)* sp. 3. The known range of the latter is from California to east Texas, and southward into northcentral Mexico. The range of *S. brevirostris* is not well documented because of a paucity of collected specimens and a problem with the location of the type locality. The type locality is cited by Coquillett (1897) as Kirkwood, Missouri, but Sabrosky and Arnaud (1965) consider the type locality to be Rhode Island because one of the syntypes bears a label inscribed with "In box with micro-larvae from R.I.". Perhaps Sabrosky and Arnaud are correct, as the only unquestionably conspecific specimen of *S. brevirostris* that I examined was collected in 1983 near Durham in Strafford Co., New Hampshire (CNC). A possibly conspecific specimen (unforunately a female and hence less easily identified) was collected from southwestern New Mexico (USNM). From such information it is apparent that *S. brevirostris* is at least present in northeast USA, and may range southwestward to Missouri or even New Mexico.

Of the other approximately 18 undescribed species of *S. (Pseudosiphona)* known to me, all are Neotropical, with greatest diversity in Chiapas (Mexico), southeastern

Brazil, and southern Peru (this pattern is due at least in part to collecting bias). Several species seem to have very wide ranges, extending from Middle America to southeastern Brazil. Unworked material includes specimens from Colombia, Venezuela, British Guiana, Bolivia, and the Caribbean islands of Trinidad and Jamaica. Records from southeastern Brazil and northern Argentina mark the known southern distributional limit of *S. (Pseudosiphona)* species.

List of described species included in *Siphona* (*Pseudosiphona*)

N   *brevirostris* Coquillett, 1897: 76. Lectotype female (**by designation in text**), USA: Missouri, Kirkwood (USNM). Lectotype examined.

List of examined, undescribed, species included in *Siphona* (*Pseudosiphona*)

S. (Pseudosiphona) sp. 1: Males and females from Chiapas, Mexico (CNC).
S. (Pseudosiphona) sp. 2: Males and females from SE Brazil (CAS, CNC, USP), males from Ecuador (CNC), Peru (CNC) and El Salvador (CAS). One possibly conspecific male from Chiapas, Mexico (CNC).
S. (Pseudosiphona) sp. 3: Males and females from California, USA (AMNH, CAS, CNC, MCZ, UCB, UKL, USNM), single males from New Mexico, USA (JEOH) and Durango, Mexico (CNC), single female from Texas, USA (CNC).
S. (Pseudosiphona) sp. 4: Males and females ranging from Sonora to Chiapas, Mexico (CAS, CNC).
S. (Pseudosiphona) sp. 5: Males from SE Brazil (CAS, CNC, USP) and Chiapas, Mexico (CNC).
S. (Pseudosiphona) sp. 6: Two males from Belize (CNC).
S. (Pseudosiphona) sp. 7: One male from SE Brazil (CNC).
S. (Pseudosiphona) sp. 8: Males from Ecuador and Peru (CNC).
S. (Pseudosiphona) sp. 9: One male from Peru (CNC).
S. (Pseudosiphona) sp. 10: One male from Chiapas, Mexico (CNC).
S. (Pseudosiphona) sp. 11: One male from Chiapas, Mexico (CNC).
S. (Pseudosiphona) sp. 12: Three males from Peru (CNC).
S. (Pseudosiphona) sp. 13: One male from SE Brazil (CNC).
S. (Pseudosiphona) sp. 14: One female from Chiapas, Mexico (CNC).
S. (Pseudosiphona) sp. 15: Males and one female from northern Argentina (CNC).
S. (Pseudosiphona) sp. 16: One female from Chiapas, Mexico (CNC).
S. (Pseudosiphona) sp. 17: One male, three females from SE Brazil (AMNH, BMNH, USP).
S. (Pseudosiphona) sp. 18: Males and females from SE Brazil (CNC, USP), single males from Ecuador (CNC), Costa Rica (USNM) and Nicaragua (USNM).
S. (Pseudosiphona) sp. 19: Three males from Amazonas, Brazil (INPA).

Siphona (subgenus *Siphona* Meigen *sensu stricto*)
Figs. 25-26, 28, 32, 34, 36, 43, 45, 67, 96, 129, 141, 144, 163.

Crocuta Meigen, 1800: 39.·Type-species, *Musca geniculata* De Geer, 1776 (by designation of Coquillett, 1910: 528). Suppressed by I.C.Z.N., 1963: 339 (Opinion 678).
Siphona Meigen, 1803: 281. Type-species, *Musca geniculata* De Geer, 1776, by designation of I.C.Z.N., 1974: 157 (Opinion 1008).
Bucentes Latreille, 1809: 339. Type-species, *B. cinereus* Latreille, 1809 (monotypy) = *Stomoxys minuta* Fabricius, 1805.
Phantasiosiphona Townsend, 1915: 93. Type-species *P. tropica* Townsend, 1915 (original designation).

Recognition

Siphona geniculata is the type species of *Siphona s.s.*, and its name literally means "geniculate siphon". The name refers to the long prementum and labella of that species, but it could just as accurately have been applied to any *Siphona s.s.* species, as all are characterized by a long proboscis, with the labella at least as long as the elongate prementum. This state has generally been regarded as unique to *Siphona s.s.* species, but is shared with some other siphonines.

Many non-*Siphona s.s.* species have slight to moderate elongation of the labella, but only in a few are they as long as the prementum. These can be discerned as non-*Siphona s.s.* species by the characteristics they share with other siphonine lineages. The several *Actia* species of this type are easily recognized by their row of katepisternal hairs and the anal vein not extended to the wing margin. The few species of *S. (Aphantorhaphopsis)* with the labella almost as long as, to slightly longer than, the prementum have fully flexible labella (not inflexible on basal half in life as in *Siphona s.s.* species) and/or a seta posteriorly on the pregonite (absent from *Siphona s.s.* species). *S. (Aphantorhaphopsis)* Nepal sp. 1 has a very long proboscis of the typical *Siphona s.s.* appearance and is the most easily misplaced species of this taxon, but can be correctly placed by its seta on the pregonite. The proboscis of *S. (Pseudosiphona)* sp. 15 is also *S. (Siphona)*-like, and several other Neotropical species of that subgenus approach this state, but these species are readily recognized by characters in the male genitalia (see Recognition section of *S. (Pseudosiphona)*). The few species of Neotropical *Siphona s.l.* species in which the labella approach the *Siphona s.s.* condition are recognized by the presence on the pregonite of a seta posteriorly and/or spinules apically.

Description

Length: 2.5-6.5mm (rarely less than 3.0mm).

Head (Figs. 25-26; ten Palearctic species shown in Mesnil 1965, figs. 150-159; North American species shown in O'Hara 1983a, figs. 1, 18-59).— Proclinate orbital setae weak to strong, subequal in length or anterior orbital longer. Eye of male small to very large, 0.62-0.91 head height; eye of female smaller than in male. Flagellomere 1 of male markedly varied in length, 0.40-0.75 head height; linear to large and almost triangular. Flagellomere 1 of female smaller than in male. Aristomere 1 short in most species, 1-2X longer than wide in some species with long flagellomere 1, 3X longer than wide in *S. trichaeta*. Aristomere 2 varied from 2.0-10.0X longer than wide, (most species between 2.5-6.0). Aristomere 3 almost bare to micropubescent, long and evenly tapered in most species, short and thickened to near tip in a few. Clypeus narrow and enclosed in membrane. Palpus long, clavate. Prementum and labella each slender and elongate; latter at least as long as prementum, inflexible on basal half or more, with pseudotracheae concentrated apically and reduced in number. Proboscis length (prementum + labella) varied from 1.3-4.8X head height (most species between 2.0-3.0).

Thorax (Figs. 28, 32, 34, 36).— Prosternum setulose or bare, varied within some species. Lower katepisternal seta longer than upper anterior seta in most species (Fig. 32), subequal in length to it in a very few. Three or four postsutural dorsocentral setae. Upper part of anepisternum with single setula in most species (Fig. 32), with two in a few. Fore tibia with preapical *ad* seta much shorter than *d* seta. Mid tibia with one *ad* seta. Tarsomeres normal in size in most species, tarsomere 5 of fore leg slightly to moderately broadened in females of a very few; claws short in most species, medium to large in a few. Wing vein CuA_1 with distal portion 0.26-0.67 length of proximal portion (*i.e. dm-cu* near wing margin; mean 0.41). Wing setulae: in most species R_1 dorsally bare or with one or two setulae distally, in a very few entirely setulose;

ventrally bare (most species) or distally setulose (a very few); R_{4+5} setulose between base and r-m in most species, beyond r-m in a few; CuA_1 bare in almost all species, with setulae in a very few (*e.g. S. lutea* and *S. bevisi*).

Abdominal terga 1-5.— Abdomen ovoid in shape in most species, markedly elongate in several Afrotropical species. T_{1+2} with or without median marginal setae (present primarily in members of *S. geniculata* group - see O'Hara 1983a: 323-4); one pair (rarely two pair) strong lateral marginal setae in most species, weak or absent in a few (weak or absent primarily in *S. maculata* group - see O'Hara 1983a: 321-322). T_3-T_5 average in most species, with extra pair of lateral marginal setae on T_3 in a few species.

Male genitalia (Figs. 67, 96, 129, 141, 144).— S_5 little varied (Fig. 67; also Andersen 1982, figs. 3-5), posterior margins of processes approximately U-shaped in most species, obtusely angled in a few; apical lobe distinctly differentiated, in a very few species apex curved inward (known only in *S. cuthbertsoni, S. mesnili* (Andersen 1982, fig. 4) and *S. oligomyia* (O'Hara 1983a, fig. 11)); median lobe rounded, relatively unmodified; processes sparsely to moderately setulose. T_6 thin to broad and dorsally continuous in most species, almost absent from a few (apparently not reduced to two lateral sclerites as in some other siphonines). Ejaculatory apodeme with fan-shaped portion 1.0-2.0X wider than hypandrial apodeme. Pregonite (Fig. 96) in profile little varied, curved anteriorly and more or less pointed apically; bare. Epiphallus absent. Distiphallus (Fig. 129) reduced posteriorly, spined anterolaterally in a few species, in profile apically rounded, truncate or pointed posteriorly; laterally incised in a very few species (*e.g.* Philippines sp. 1). Postgonite apically rounded. Surstylus (Fig. 141, 144) average length to slightly elongate, more or less straight; basally free from epandrium. Cerci (Fig. 141, 144) average length, smoothly curved at midlength; moderately setose on basal half.

Examined male genitalia of: *S. akidnomyia, S. brunnea, S. collini, S. confusa, S. cristata, S. cuthbertsoni, S. flavifrons, S. futilis, S. geniculata, S. illinoiensis, S. ingerae, S. intrudens, S. kairiensis, S. longissima, S. lurida, S. lutea, S. macronyx, S. maculata, S. medialis, S. multifaria, S. nigricans, S. oligomyia, S. pacifica, S. paludosa, S. pauciseta, S. pisinnia, S. rizaba, S. setosa, S. tropica, S. unispina*, Ecuador spp. 1-3, Kenya spp. 1-2, Nepal sp. 1, Philippines sp. 1 and Taiwan sp. 1. Examined published figures of: *S. hungarica* (Andersen 1984, figs. 1-3), *S. kairiensis* (O'Hara 1983b, figs. 3-5), North American *Siphona* species (O'Hara 1983a, figs. 60-80), and European *Siphona* species (aedeagus only, Andersen 1982, figs. 2, 18-28, and Andersen 1983, fig. 21). Male reproductive system of *S. cristata* shown in Andersen (1983, fig. 1).

Female genitalia (Figs. 43, 45).— Short. S_6 with average length hairs. T_6 absent; spiracles of segment 6 in membrane dorsal to anterolateral margins of S_6. S_7 with long anterior apodeme; not posteromedially keeled. T_7 absent; spiracles of segment 7 in membrane dorsal to anterolateral margins of S_7. S_8 distinctly developed, haired. T_{10} absent or very slightly sclerotized.

Female genitalia of *S. melanura* (examined externally but not dissected) are uniquely modified, in marked contrast to the conservative features in other members of the subgenus. S_6 is longer than wide, shovel-like, extremely smooth and shiny black, apically rounded, with hairs confined to single row on membrane along posterior edge of sternum. S_6 in form of flap-like covering over similarly-shaped, apically more sharply-rounded, blade-like S_7.

Examined female genitalia of: *S.* nr. *intrudens, S. lutea, S. maculata, S. nigricans, S. pisinnia* and *S.* nr. *tropica*. Examined published figures of: *S. hungarica* (Andersen 1983, fig. 4), *S. nigricans* (fig. 12 in O'Hara 1983a, as *S. hokkaidensis*) and *S. setosa* (Andersen 1982, fig. 6, and Andersen 1983, fig. 7). Female reproductive system of *S. ingerae* shown in Andersen (1983, fig. 2).

Taxonomic changes

Siphona nigrohalterata Mesnil.— Among the new siphonines described by Mesnil in his 1959 paper about tachinids of East Africa were *Siphona amplicornis amplicornis* and *Siphona amplicornis nigrohalterata* (pp. 21-22). The types (both male) were collected from West Kibo, Nigeria - the former at 2800m between 17-22.IV.1952 and the latter at 3500m between 23-30.IV.1952. These "subspecies" do not seem to be geographically or temporally isolated, as a paratype of *S. a. amplicornis* bears the same locality data as the type of *S. a. nigrohalterata*. I infer from this that these sympatric "subspecies" either freely interbreed (*i.e.* cannot be

regarded as separate subspecies) or are reproductively isolated (*i.e.* represent two species). Examination and comparison of the holotypes suggest the latter; the type of *S. a. nigrohalterata* has a slightly longer proboscis, less elongate abdomen, shorter abdominal setae, and markedly different coloration (particularly on the abdomen). These differences are not major, but in total are not atypical of closely related *Siphona* species. Thus I conclude that *S. nigrohalterata* is probably a valid species reproductively isolated from *S. amplicornis.*

Synonymy of Siphona janssensi (Mesnil) with Siphona cuthbertsoni Curran.— *S. cuthbertsoni* is more easily recognized than most African *Siphona* species because of its very large eye, rather short flagellomere 1, proboscis length less than 2.5X head height, and generally dark color (including abdomen entirely dark in ground color). It is probable that Mesnil was unfamiliar with this species of Curran's, except perhaps by name, as he did not mention it in his work about the *Siphona* of the "Belgian Congo".

Specimens of *S. cuthbertsoni* identified by direct comparison with the male holotype of that species were later compared with the male holotype of *S. janssensi.* On the basis of these comparisons, the name *S. janssensi* is here synonymized with that of *S. cuthbertsoni.*

Note about use of the subspecific category.— Subspecies have rarely been described in the Siphonini, though Mesnil occasionally used this category for taxa displaying slight morphological differences. Mesnil's concept of subspecies was not based on geographic (and hence I assume not reproductive) isolation. I examined the types of most of Mesnil's subspecies and have reclassified their names as synonyms or separate species. However, I was unable to examine the types of several subspecies of *Siphona fuliginea* Mesnil and *Siphona reducta* (Mesnil). I leave these taxa as classified by Mesnil pending study of the types.

Status of Siphona unispina (Mesnil) and Siphona unispina infuscata (Mesnil).— In 1952 Mesnil revised the *Siphona* species of the "Belgian Congo", naming many new species and one pair of subspecies: *S. unispina unispina* and *S. unispina infuscata* (Mesnil 1952a). As was Mesnil's practice, these subspecies were recognized exclusively on morphological criteria without the now standard requirement of at least partial spatial or temporal separation. Type localities of these taxa are separated by less than 150km, with paratypes of both collected at one intermediate locality. This suggests that the subspecific category is inappropriate, and that the names *S. u. infuscata* and *S. unispina* are synonyms or *S. u. infuscata* is specifically distinct. Crosskey (1980) chose the former, but upon comparison of the types of both taxa I have decided to recognize *Siphona infuscata* as a valid species, based upon three characteristics that differ between the types: 1) proboscis length of *S. unispina* is 3.5X head height as compared with 4.3X head height in *S. infuscata,* 2) thorax of *S. unispina* is bluish gray, in *S. infuscata* mostly brown, and 3) R_{4+5} is setulose beyond *r-m* in *S. unispina* and not beyond *r-m* in *S. infuscata.* Abdominal characteristics and especially male genitalia cannot be compared between types

because the abdomen of the type of *S. unispina* is missing. Paratypes were not examined, but a male specimen from the Bwamba river area (SE Zaire) identified by Mesnil as *S. unispina* fits the description of that species and possesses the three characteristics listed above for distinguishing *S. unispina* from *S. infuscata*.

Hosts

Most hosts of *Siphona s.s.* are species of the Noctuidae, and all known lepidopteran hosts belong to the Macrolepidoptera (Table 2). Some members of the *S. geniculata* group are parasites of crane fly larvae (Tipulidae), and are unique in this habit in the Siphonini and among the few tachinids that parasitize other Diptera.

Phylogenetics

The long, geniculate proboscis of *Siphona s.s.* species, with labella at least as long as the elongate prementum, is synapotypic of the subgenus. Elongation of the proboscis has occurred independently in many siphonine lineages, but only in *Siphona s.s.* species are the labella rigid (in life) on basal half or more and at least as long as the prementum in all species. Hence this condition is considered the groundplan (and synapotypic) state of *Siphona s.s.*, and a shorter (with a few exceptions padlike) labella the groundplan state of other siphonine lineages.

Andersen (1983) also considered the reduced number of pseudotracheae in *Siphona s.s.* species as a synapotypy of the subgenus, but this state is not treated separately here because for many species it is (in siphonines) directly correlated with elongation of the labella. For example, padlike labella may have about 15 pair of pseudotracheae, elongate labella of *S. (Siphonopsis)* species (Fig. 18) about eight pair, and the long labella of *Siphona s.s.* species about four pair. This correlation is not constant as certain species of *S. (Aphantorhaphopsis)*, for instance, with elongate labella have relatively numerous pseudotracheae. The trend is nevertheless evident, and because of this the number of pseudotracheae on the labella is not treated as a separate character in this study. No other synapotypies of *Siphona s.s.* species are known. The included species have a number of shared characteristics, of which male genitalic similarities are particularly marked (see figs. 60-80 in O'Hara 1983a), and these are congruent with the hypothesis of monophyly of this group. The few other siphonines with a *S. (Siphona)*-like proboscis are recognized as non-members of that group by synapotypies they share with other taxa, and their non-*S. (Siphona)*-like male genitalia.

Andersen's (1982) revision of European *Siphona s.s.* species went to press at about the time I completed a revision of the North American *Siphona s.s.* species (O'Hara 1983a). Therefore my comparison of Nearctic and Palearctic species of *Siphona s.s.*, and discussion of species groups, did not include the four new European *Siphona s.s.* species described by him. Here I briefly mention the species groups to which Andersen's species belong: *S. ingerae* is a member of the *S. maculata* group, and is closely related to the North American species *S. intrudens*; *S.*

martini is now considered conspecific with *S. nigricans* (Andersen, pers. comm.), and is a member of the *S. geniculata* group; and *S. mesnili* and *S. variata* are placed in the *S. geniculata* group (formerly called the *S. cristata* group), because these species were considered by Andersen (*op. cit.*) to be close to *S. confusa*. Andersen's new species from Hungary, *S. hungarica* (Andersen 1984), is closely related to *S. ingerae* and *S. intrudens*, and belongs to the *S. maculata* group.

Geographic distribution

Siphona s.s. is widely distributed, with 84 described species. Forty-one of these are Afrotropical in distribution (see Crosskey 1980 for ranges; partial key in Mesnil 1952a), with more species recorded from Madagascar than any other siphonine taxon (Mesnil 1977a). Three apparently endemic species are on Madagascar and five species are shared with the mainland (Crosskey 1980), suggesting that *Siphona s.s.* includes some markedly vagile members. This suggestion is further evidenced by the presence of *Siphona s.s.* species on the Juan Fernández Islands west of Chile, the Canary Islands, and four species with Holarctic distributions (excluding *S. geniculata*, introduced by man to North America). It is therefore rather surprising that *Siphona s.s.*, with 41 species in the Afrotropical region and 20 in the Palearctic region, has only three described species in the Oriental region (Crosskey 1976a) and one in the Australian region (O'Hara 1983b). From examined material (and Shima, pers. comm.), the Oriental region and probably islands of the Indoaustralian archipelago north of Australia contain at least a modest number of undescribed species. There is as yet no indication of more than one *Siphona s.s.* species in Australia.

Palearctic *Siphona s.s.* species are best known in England (Crosskey 1976b) and Europe, and are keyed in Mesnil (1964) and Andersen (1982). Additional records are cited in Mesnil and Pschorn-Walcher (1968), Herting (1968b, 1969b, 1973), Draber-Mońko (1978, 1981), Kugler (1979), Richter (1971, 1975, 1976a,b, 1980, 1986), Richter and Khitsova (1982), Chao and Shi (1982), Karczewski (1983), Mihályi and Weinberg (1984) and Rognes (1986), and distributions are summarized in Herting (1984).

Twenty-one *Siphona s.s.* species are in North America (including "Middle America"). These were recently revised and their distributions discussed in O'Hara (1983a). Only two exclusively South American *Siphona s.s.* species are described, but there are specimens of at least ten undescribed species among material I have examined.

List of described species included in *Siphona (Siphona)*

A   *abbreviata* (Villeneuve), 1915: 199 (*Bucentes*). Female syntypes, Madagascar: Sikora (NMV). Syntypes examined.

N,S *akidnomyia* O'Hara, 1983a: 311. Holotype male, Mexico: Chiapas, Mt.

Zontehuitz (CNC). Holotype examined.

A   *albocincta* (Villeneuve), 1942a: 55 (*Bucentes*). Holotype female, Zaire: Nylragongo (CNC). Holotype examined.

A   *amoena* (Mesnil), 1952a: 12 (*Crocuta*). Holotype male, Zaire: Karisimbi (MRAC). Holotype examined.

A   *amplicornis* Mesnil, 1959: 21. Holotype male, Tanzania: West Kibo (SMNS). Holotype examined.

A   *angusta* Mesnil, 1959: 22. Holotype male, Tanzania: West Kibo (SMNS). Holotype examined.

A   *antennalis* (Mesnil), 1952a: 9 (*Crocuta*). Holotype male, Zimbabwe: Salisbury (CNC).

A   *atricapilla* Mesnil, 1959: 20. Holotype male, Tanzania: West Kibo (SMNS). Holotype examined.

A   *bevisi* Curran, 1941: 7. Holotype male, South Africa: Natal, Durban (AMNH). Holotype examined.

A   *bilineata* (Mesnil), 1952a: 10 (*Crocuta*). Holotype male, Rwanda: Niabirehe (MRAC). Holotype examined.

P   *boreata* Mesnil, 1960: 190. Holotype male, Federal Republic of Germany: Arnsberg (CNC). Holotype examined.

S   *brunnea* O'Hara, 1983a: 308. Holotype male, Mexico: Chiapas, Mt. Zontehuitz (CNC). Holotype examined.

A   *capensis* Curran, 1941: 7. Holotype female, South Africa: East London (PPRI). Holotype examined.

P   *collini* Mesnil, 1960: 188. Holotype male, Great Britain: Cambridgeshire, Burwell (HDE). Holotype examined.

P   *confusa* Mesnil, 1961: 201. Holotype male, Sweden: Gränna (CNC). Holotype examined.

A   *cothurnata* (Mesnil), 1952a: 17 (*Crocuta*). Holotype male, Rwanda: Burambi (MRAC). Holotype examined.

A   *creberrima* (Speiser), 1910: 142 (*Crocuta*). Syntypes, Tanzania: Kilimanjaro (NRS). Syntypes examined.

P,N *cristata* (Fabricius), 1805: 281 (*Stomoxys*). Holotype female, Denmark: Zealand (ZMUC). Holotype examined.

      syn.   *palpina* Zetterstedt, 1859: 6064. Holotype female, Sweden: Lindholmen (UZI).— Mesnil, 1964: 861.

                      chetoliga Rondani, 1865: 194. Holotype female, Italy (MZF).— Herting, 1969a: 192.

                      chaetolyga. Incorrect subsequent spelling of *chetoliga* Rondani (Herting, 1969a: 192).

A   *cuthbertsoni* Curran, 1941: 7. Holotype male, Zimbabwe: Salisbury (AMNH). Holotype examined.

      syn.   *janssensi* (Mesnil), 1952a: 4 (*Crocuta*). Holotype male (abdomen

missing), Rwanda: Kibga (MRAC). Holotype examined. **New synonymy.**

P   *efflatouni* Mesnil, 1960: 188. Holotype female, Egypt: Mariout (CNC). Holotype examined.

P   *flavifrons* Staeger *in* Zetterstedt, 1849: 3211. Lectotype female (by designation of Andersen, 1982: 167), Denmark: North East Zealand, Ordrup (ZMUC). Lectotype examined.

N   *floridensis* O'Hara, 1983a: 288. Holotype male, USA: Florida, Orlando (AMNH). Holotype examined.

O   *foliacea* (Mesnil), 1953: 113 (*Crocuta* (*Siphona*)). Holotype male, Burma: Kambaiti (ZMU). Holotype examined.

A   *fuliginea* Mesnil, 1977a: 77. Holotype male, Madagascar: Ambatolahy (MNHN).

    ssp.   *cerina* Mesnil, 1977a: 76. Holotype male, Madagascar: Amber Mtn. (MNHN).

                  rubea Mesnil, 1977a: 77. Holotype male, Madagascar: Manjakatompo (MNHN).

N,S *futilis* Wulp, 1890: 125. Lectotype male (by designation of O'Hara, 1983a: 305), Mexico: Guerrero, Omilteme (BMNH). Lectotype examined.

    syn.   *ceres* (Curran), 1932: 14 (*Bucentes*). Holotype female, Guatemala: Antigua (AMNH).— O'Hara, 1983a: 305. Holotype examined.

O   *gedeana* Wulp, 1896: 109. Holotype female, Indonesia: Java, Goenoeng Gedeh (lost, see Crosskey, 1976a: 214).

    syn.   *nigripalpis* (de Meijere), 1924: 223 (*Bucentes*). Lectotype male (by designation of Crosskey, 1969: 89), Indonesia: Java, Pangrango (ZMA). Lectotype examined.

P,N *geniculata* (De Geer), 1776: 38 (*Musca*).[2] Three syntypes, Sweden (NRS; types erroneously listed as lost in Andersen 1982 and O'Hara 1983a).

    syn.   *urbanis* (Harris), 1780: 153 (*Musca*). Type, England (lost).— Crosskey, 1976b: 100.

                  minuta (Fabricius), 1805: 282 (*Stomoxys*). Holotype female (head missing), Denmark (ZMUC).— Herting, 1984: 125. Holotype examined.

                  cinerea (Latreille), 1809: 338 (*Bucentes*). Type(s), France: Paris (not located).— Herting, 1984: 125.

                  cinerea Meigen, 1824: 156. Holotype female, Europe (MNHN).— Herting, 1972: 4.

                  tachinaria Meigen, 1824: 156. Holotype male, Federal Republic of Germany: Nordrhein, Aachen (MNHN).— Herting, 1972: 13.

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[2]Page 20 is cited by various authors for the description of *S. geniculata*, but this apparently refers to the German translation of De Geer's work by Goeze in 1782 (Herting, *in litt.*).

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      analis Meigen, 1824: 157. Holotype male, Europe (MNHN).—
Herting, 1972: 3.

      nigrovittata Meigen, 1824: 157. Holotype male (MNHN).— Herting,
1972: 11.

      meigenii (Lepeletier and Serville *in* Latreille, et al.), 1828: 501
(*Bucentes*). Replacement name for *S. cinerea* Meigen, 1824
(objective synonym).— Herting, 1984: 125.

A   *gracilis* (Mesnil), 1952a: 13 (*Crocuta*). Holotype male (head missing), Rwanda:
Kibga (MRAC). Holotype examined.

P   *grandistylum* Pandellé, 1894: 108. Holotype male, France: Pyrenees (MNHN).

P   *griseola* Mesnil, 1970: 118 (as subspecies of *S. maculata* Staeger). Holotype
male, Israel: Tel Aviv (CNC). Holotype examined.

P   *hungarica* Andersen, 1984: 5. Holotype male, Hungary: Hortobàgy N.P.
(HNHM). Paratype examined.

N   *illinoiensis* Townsend, 1891: 368. Lectotype male (by designation of O'Hara,
1983a: 307), USA: Illinois (UKL). Lectotype examined.

A   *infuscata* (Mesnil), 1952a: 14 (as subspecies of *Crocuta unispina* Mesnil).
Holotype male, Zaire: Tshamugussa (MRAC). Holotype examined. **New status**.

P   *ingerae* Andersen, 1982: 161. Holotype male, Denmark: North East Zealand,
Bagsvaerd, Smørmose (ZMUC). Holotype examined.

N   *intrudens* (Curran), 1932: 14 (*Bucentes*). Holotype male, USA: Pennsylvania,
Castle Rock (AMNH). Holotype examined.

U   *kairiensis* O'Hara, 1983b: 79. Holotype male, Australia: Queensland, Tinaroo
Lake (CAS). Holotype examined.

S   *kuscheli* (Cortés), 1952: 110 (*Phantasiosiphona*). Holotype male, Juan
Fernandez Islands: Masatierra (CIE). Holotype examined.

A   *laticornis* Curran, 1941: 9. Holotype male, South Africa: Pretoria (PPRI).
Holotype examined.

A   *lindneri* Mesnil, 1959: 22. Holotype male, Tanzania: Msingi (SMNS). Holotype
examined.

N,S *longissima* O'Hara, 1983a: 311. Holotype male, Mexico: Chiapas, San
Cristobal (CNC). Holotype examined.

N,P *lurida* Reinhard, 1943: 20. Holotype male, USA: Oregon, Rainier (CNC).
Holotype examined.

N   *lutea* (Townsend), 1919: 584 (*Crocuta*). Lectotype female (by designation of
O'Hara, 1983a: 296), USA: New Hampshire, Franconia (USNM). Lectotype
examined.

      syn.   *tenuis* Curran, 1933b: 10. Holotype male, Canada: Ontario,
Timagami (AMNH).— O'Hara, 1983a: 296. Holotype examined.

N   *macronyx* O'Hara, 1983a: 313. Holotype male, USA: Washington, Pullman
(WSUP). Holotype examined.

P,N *maculata* Staeger *in* Zetterstedt, 1849: 3212. Lectotype male (by designation of

Andersen, 1982: 162), Denmark: North East Zealand, Charlottenlund (ZMUC). Lectotype examined.

N *medialis* O'Hara, 1983a: 303. Holotype male, Canada: Nova Scotia, Cranberry Island (CNC). Holotype examined.

A *melania* (Bezzi), 1908: 58 (*Bucentes*). Holotype female, Ethiopia (not located).

A *melanura* Mesnil, 1959: 23. Holotype female, Tanzania: West Kibo (SMNS). Holotype examined.

P *mesnili* Andersen, 1982: 163. Holotype male, Denmark: North East Zealand, Gribskov, Harager Hegn (ZMUC). Holotype examined.

N *multifaria* O'Hara, 1983a: 293. Holotype male, Canada: Yukon, Dempster Hwy., mi. 87 (CNC). Holotype examined.

A *munroi* Curran, 1941: 6. Holotype female, South Africa: Fort Jackson (PPRI). Holotype examined.

A *murina* (Mesnil), 1952a: 15 (*Crocuta*). Holotype male, Zaire: Nyongera (MRAC). Holotype examined.

P,N *nigricans* (Villeneuve), 1930: 100 (*Bucentes*). Holotype male, Sweden: Gallivara (CNC). Holotype examined.

      syn.   *hokkaidensis* Mesnil, 1957: 36. Holotype female, Japan: Hokkaido, Obihiro (CNC).— Herting, 1982: 8. Holotype examined.

              silvarum Herting, 1967a: 9. Holotype male, Federal Republic of Germany: Freiburg (CNC).— Herting, 1982: 8. Holotype examined.

              martini Andersen, 1982: 169. Holotype male, Sweden: Scania, Hyllstofta (UZI).— Andersen (pers. comm.). Paratype examined.

A *nigrohalterata* Mesnil, 1959: 22 (as ssp. of *S. amplicornis* Mesnil). Holotype male, Tanzania: West Kibo (SMNS). Holotype examined. **New status**.

A *nigroseta* Curran, 1941: 8. Holotype female, South Africa: Pretoria (PPRI). Holotype examined.

O *nobilis* (Mesnil), 1953: 112 (*Crocuta* (*Siphona*)). Holotype male, Philippines: Mont Palis (ZMU). Holotype examined.

A *obesa* (Mesnil), 1952a: 8 (*Crocuta*). Holotype male, Zaire: Rwindi (MRAC). Holotype examined.

A *obscuripennis* Curran, 1941: 8. Holotype female, Zimbabwe: Vumba Mts. (AMNH). Holotype examined.

N *oligomyia* O'Hara, 1983a: 297. Holotype male, Canada: British Columbia, Keremeos (CNC). Holotype examined.

N *pacifica* O'Hara, 1983a: 291. Holotype male, USA: Washington, Dartford (WSUP). Holotype examined.

P *paludosa* Mesnil, 1960: 188. Holotype male, USSR: Tolmatschevo, Luga (ZIL). Holotype examined.

A *patellipalpis* (Mesnil), 1952a: 10 (*Crocuta*). Holotype male, Zaire: Mt. Sesero (MRAC). Holotype examined.

P *pauciseta* Rondani, 1865: 193. Eight syntypes, Italy (MZF; mixed series

according to Herting, 1969a: 198).

    syn.   *oculata* Pandellé, 1894: 108.— Lectotype male (by designation of Herting, 1978: 6), France (MNHN).

            delicatula Mesnil, 1960: 190. Holotype male, Great Britain: Chippenham (HDE).— Herting, 1969a: 198. Holotype examined.

A *phantasma* (Mesnil), 1952a: 7 (*Crocuta*). Holotype male, Rwanda: Gahinga (MRAC). Holotype examined.

A *pigra* Mesnil, 1977a: 78. Holotype female, Madagascar: Moramanga (MNHN).

N,S *pisinnia* O'Hara, 1983a: 298. Holotype male, USA: New Mexico, 21km. n. Silver City (CNC). Holotype examined.

S *pseudomaculata* Blanchard, 1963: 233. Syntypes, Argentina: Santa Fe (MBR). Syntypes examined.

A *reducta* (Mesnil), 1952a: 18 (*Crocuta*). Holotype male, Zaire: Tshamugussa (MRAC). Holotype examined.

    ssp.   *ludicra* Mesnil, 1977a: 78. Holotype male, Madagascar: Manjakatompo (MNHN).

N,S *rizaba* O'Hara, 1983a: 310. Holotype male, Mexico: Veracruz, Orizaba (MSU). Holotype examined.

P *rossica* Mesnil, 1961: 202. Holotype male, USSR: Leningrad, Lugsk (ZIL). Holotype examined.

A *rubrapex* Mesnil, 1977a: 79. Holotype female, Madagascar: Perinet (MNHN).

A *rubrica* (Mesnil), 1952a: 11 (*Crocuta*). Holotype male, Zaire: Rutshuru (MRAC). Holotype examined.

A *setinerva* (Mesnil), 1952a: 16 (*Crocuta*). Holotype male, Rwanda: Kibga (MRAC). Holotype examined.

P *setosa* Mesnil, 1960: 191. Holotype male, USSR: Tolmatschevo, Luga (ZIL). Holotype examined.

P *seyrigi* Mesnil, 1960: 189. Holotype male, Canary Islands: Tenerife (MNHN). Holotype examined.

A *simulans* (Mesnil), 1952a: 18 (*Crocuta*). Holotype male, Rwanda: Kundhuru-ya-Tshuve (MRAC). Holotype examined.

A *sola* Mesnil, 1959: 21. Holotype male, Tanzania: Usangi (SMNS). Holotype examined.

A *spinulosa* (Mesnil), 1952a: 12 (*Crocuta*). Holotype male, Zaire: Ngesho (MRAC). Holotype examined.

A *trichaeta* (Mesnil), 1952a: 18 (*Crocuta*). Holotype male, Rwanda: Karisimbi (MRAC). Holotype examined.

N,S *tropica* (Townsend), 1915: 93 (*Phantasiosiphona*). Holotype male, Mexico: Veracruz, San Rafael (USNM). Holotype examined.

A *unispina* (Mesnil), 1952a: 14 (*Crocuta*). Holotype male (abdomen missing), Zaire: Rutshuru (MRAC). Holotype examined.

P *variata* Andersen, 1982: 164. Holotype male, Denmark: Frederikshavn

(ZMUC). Holotype examined.

A   *vittata* Curran, 1941: 8. Holotype male, Zimbabwe: Salisbury (AMNH). Holotype examined.

A   *vixen* Curran, 1941: 9. Holotype female, Zimbabwe: Salisbury (AMNH). Holotype examined.

A   *wittei* (Mesnil), 1952a: 5 (*Crocuta*). Holotype male, Rwanda: Karisimbi (MRAC). Holotype examined.

Nomina dubia

P   *analis* Robineau-Desvoidy, 1830: 92. Type(s), France (lost).

P   *clausa* Robineau-Desvoidy, 1850: 209. Holotype male, France (lost).

P   *consimilis* Robineau-Desvoidy, 1850: 205. Holotype male, France (lost).

P   *fuscicornis* Robineau-Desvoidy, 1850: 205. Syntypes, France (lost).

P   *humeralis* Robineau-Desvoidy, 1850: 207. Syntypes, France (lost).

P   *maculipennis* Meigen, 1830: 365. Holotype, Portugal: Algarve (lost).

P   *melanocera* Robineau-Desvoidy, 1850: 206. Holotype female, France (lost).

P   *pusilla* Robineau-Desvoidy, 1830: 92. Type(s), France: Paris (lost).

    syn.   *persilla*. Incorrect subsequent spelling of *pusilla* Robineau-Desvoidy (Coquillett, 1897: 76).

P   *quadrinotata* Robineau-Desvoidy, 1850: 203. Holotype female, France (lost).

    syn.   *quadricincta*. Incorrect subsequent spelling of *quadrinotata* Robineau-Desvoidy (Rondani, 1859: 10).

P   *silvatica* Robineau-Desvoidy, 1850: 208. Holotype male, France (lost).

P   *testacea* Robineau-Desvoidy, 1850: 207. Holotype male, France (lost).

P   *tristis* Robineau-Desvoidy, 1850: 203. Holotype female, France (lost).

Nomina nuda

S   *anthomyformis* Lynch Arribálzaga *in* Brauer, 1898: 505 (13).

P   *dorsalis* Brauer and Bergenstamm, 1891: 410.

P   *pauciseta* Mesnil, 1964: 856 (as ssp. of *S. geniculata*).

O   *taiwanica* (Baranov *in* Hennig), 1941: 195 (*Crocuta*).

List of examined, undescribed, species included in *Siphona* (*Siphona*)

S. (Siphona) nr. *intrudens*: Females from Alberta, Canada (JEOH).

S. (Siphona) nr. *tropica*: One female from Coquimbo, Chile (CNC).

S. (Siphona) Ecuador sp. 1: One male from sw. Alausi, Chimborazo (CAS).

S. (Siphona) Ecuador sp. 2: One male from Cerro Pelado, Carchi (CNC).

S. (Siphona) Ecuador sp. 3: One male from sw. Banos (CAS).

S. (Siphona) Kenya sp. 1: One male from Mt. Kenya, Nanyuki (CAS).

S. (Siphona) Kenya sp. 2: Males and females from Kenya and Tanzania (CAS).

S. *(Siphona)* Nepal sp. 1: One male from 28°00'N 85°00'E (CNC).
S. *(Siphona)* Philippines sp. 1: One male from Mt. Apo, Mindanao (BLKU).
S. *(Siphona)* Taiwan sp. 1: One male from Mt. Alishan (BLKU).
Many undescribed species of *S. (Siphona)* examined from South America.

Siphona (subgenus *Siphonopsis* Townsend)
Figs. 18, 24, 30, 97-98, 130.

Siphonopsis Townsend, 1916: 622. Type-species, *Siphona plusiae* Coquillett, 1895 (original designation).
New subgeneric status in *Siphona* Meigen.

Recognition

This homogeneous group of three described and approximately 13 undescribed species is New World in distribution, with greatest diversity in the Neotropics.

The male genitalia of *S. (Siphonopsis)* species possess the only states which are unique to this taxon, though the following external characteristics distinguish adults of this taxon from those of most other New World *Siphona s.l.* species: abdomen generally dark in ground color on T_4 and T_5 and medially on T_3, with moderate pruinosity (sparse pruinosity in a few species, and resembling abdomen of most *S. (Pseudosiphona)* species); (head of *S. plusiae* shown in Fig. 18) parafacial with several hairs below lowest frontal seta (as in most *Siphona s.l.* species, but different from the more haired parafacial of most *S. (Pseudosiphona)* species); arista almost bare in most species (also in contrast to the haired arista of most *S. (Pseudosiphona)* species); labella of proboscis elongate, varied from two-thirds prementum length to slightly less than prementum length; three postsutural dorsocentral setae; lower katepisternal seta longer than upper anterior one; wing vein R_{4+5} not setulose beyond crossvein *r-m* and CuA_1 bare.

The most import;nt diagnostic feature of *S. (Siphonopsis)* species externally is labella length. As mentioned above, it varies from two-thirds prementum length to slightly less than prementum length. This feature distinguishes members of this taxon from those of *Siphona s.s.*, in which the labella are at least as long as the prementum. Of several minor external differences between members of *S. (Siphonopsis)* and *S. (Pseudosiphona)* (*cf.* Recognition sections), one of the better is the slightly shorter labella of most (though not all) *S. (Pseudosiphona)* species. Since several other *Siphona s.l.* species have labella as elongate as in *S. (Siphonopsis)* species, it is necessary to examine the male genitalia of *S. (Siphonopsis)*-like specimens for a reliable identification. It is not possible to reliably identify adult females of all New World *Siphona s.l.* species.

Adult males with the above external characteristics are recognized as members of *S. (Siphonopsis)* by the following genitalic states: sternum 5 with apex of apical lobe curved inward; pregonite (Figs. 97-98) slender to average in width, lacking spinules anterolaterally, with (most species) or without (a few species) tiny seta posteriorly (medium-sized seta in a few species); distiphallus little varied, in profile

tapered to narrow truncate tip in most species (Fig. 130), more elongate and lateral apices separated in a few species; cerci not sharply inflexed at midpoint. The unique shape of the distiphallus of *S. (Siphonopsis)* species readily separates males with the above external characteristics from males of other *Siphona s.l.* lineages. Most likely to be confused externally with *S. (Siphonopsis)* species are several species of *S. (Pseudosiphona)*, but features of the pregonite, distiphallus and cerci unequivocally separate males of these subgenera. Similarly, the few other *Siphona s.l.* species with *S. (Siphonopsis)*-like labella (see Table 1) differ in male genitalic states (most important of which is distiphallus shape).

Description

Length: 2.5-4.5mm.

Head (Figs. 18, 24, 30).— Proclinate orbital setae subequal in length or anterior one longer. Eye of male medium to medium-large, 0.73-0.84 head height; eye of female subequal to slightly larger than in male. Flagellomere 1 of male short to medium-long, 0.37-0.65 head height; shape from average width to large and triangular. Flagellomere 1 of female smaller than in male in most species, subequal in a few. Aristomere 1 short in most species, as long as wide in at least two species. Aristomere two 1.5-6X longer than wide. Aristomere 3 short to long and evenly tapered, almost bare to short plumose. Clypeus narrow and enclosed in membrane. Palpus short, clavate. Proboscis (Figs. 18, 24, 30) with prementum short to medium in length, between 0.6-0.7 head height in most species (not more than about 0.75 head height), labella elongate, 0.7-0.9 prementum length and inflexible in life on about basal third.

Thorax.— Prosternum setulose. Lower katepisternal seta longer than upper anterior seta. Three postsutural dorsocentral setae. Upper part of anepisternum with single setula. Fore tibia with preapical *ad* seta much shorter than *d* seta. Mid tibia with one *ad* seta. Claws short. Wing vein CuA_1 with distal portion 0.29-0.55 length of proximal portion (mean 0.43). Wing setulae: R_1 dorsally bare, or distally setulose, ventrally bare; R_{4+5} setulose between base and *r-m*; CuA_1 bare.

Abdominal terga 1-5.— Abdomen ovoid in shape. T_{1+2} without median marginal setae, lateral marginal setae absent or weakly developed. T_3-T_5 with average setation.

Male genitalia (Figs. 97-98, 130).— S_5 with posterior margins of processes approximately U-shaped; apical lobe large and distinctly differentiated, apex curved inward; median lobe broadly rounded to truncate and relatively unmodified in most species, with accessory lobe slightly to distinctly differentiated in a very few species (distinctly differentiated only in *S. conata*); processes moderately setulose. T_6 varied from two lateral sclerites to single dorsally continuous sclerite. Ejaculatory apodeme with fan-shaped portion 1.0-2.0X width of hypandrial apodeme. Pregonite (Figs. 97-98) in profile curved anteriorly and more or less pointed apically, in a few species rather slender (Fig. 98); tiny to medium seta posteriorly in most species, seta absent from at least two species. Epiphallus absent. Distiphallus (Fig. 130) reduced posteriorly, not incised laterally, without enlarged spines anteriorly or laterally, in profile tapered to a narrow truncate tip, in a few species distiphallus elongate and very narrow, with apex deeply incised anteriorly and posteriorly (*i.e.* distiphallus with two long arms in posterior view). Postgonite reduced in *S. conata*, short to average length in other species, apically rounded or pointed. Surstylus about average length in most species, elongate in *S. conata*, straight in most species, slightly curved posteriorly in a few; basally free from epandrium. Cerci average length in most species, rather short in a few, in profile average width to thick; moderately setose on basal half.

Examined male genitalia of: *S. conata, S. plusiae, S. (Siphonopsis)* spp. A-I,K-N.

Female genitalia.— Short. S_6 with average length hairs. T_6 absent, or present as two tiny to small lateral sclerites or a single median sclerite; spiracles of segment 6 in membrane dorsal to lateral margins of S_6 or in lateral sclerites of T_6. S_7 with long anterior apodeme in most species, short in a few; flat and unmodified in most species, in *S. conata* elongate and keeled posteromedially and apically incised. T_7 absent in most species, present as two tiny lateral sclerites in *S. conata*; spiracles of segment 7 in membrane between segments 6 and 7. S_8 distinctly developed, haired. T_{10} present as median sclerite in most species, as two sclerites in a very few.

Examined female genitalia of: *S. conata, S. plusiae, S. (Siphonopsis)* spp. A,B,E,M and N.

Hosts

   S. conata and *S. plusiae* attack a serious pest of oak, the California oakworm (*Phryganidia californica*). *S. plusiae* is also recorded from two other insect pests in California, the cabbage looper (*Trichoplusia ni*) and alfalfa looper (*Autographa californica*) (Table 2). Though attacking economically important pest species, *S. conata* and *S. plusiae* do not parasitize their hosts at sufficient densities to be considered good biological control agents.

   S. brasiliensis is listed as a parasitoid of two noctuid species in South America (Table 2). However, the name might be a misidentification because *S. (Siphonopsis)* is very diverse in South America and *S. brasiliensis* is the only described species.

Phylogenetics

   The distiphallus of males of *S. (Siphonopsis)* species is narrowed to a truncate tip (Fig. 130). The uniqueness of this state within the Siphonini, and its uniformity thoughout the subgenus, provides the best evidence for monophyly of this taxon. A number of other similarities externally and in the male genitalia also suggest that the included species are closely related; however, none can be defended as synapotypic of *S. (Siphonopsis)*. For instance, adults of *S. (Siphonopsis)* species have characteristically elongate labella (Fig. 18), which are shorter (relative to prementum length) than in *Siphona s.s.* species and longer than in most *S. (Pseudosiphona)* species. However, because this state is also present in several other *Siphona s.l.* species belonging to several lineages (see Table 2), it is possible that this state is not independently derived in *S. (Siphonopsis)* but rather synapotypic of this taxon and one of these lineages. Much convergence has occurred among *Siphona s.l.* lineages in the development of elongate labella, so this character can not be used reliably for the grouping of the supraspecific taxa of this genus.

Geographic distribution

   Three described and at least 13 undescribed species are included in *S. (Siphonopsis)*. *S. plusiae* is the most widely distributed of the described species, ranging in the west from Oregon to southern Mexico. A closely related, undescribed, species is sympatric with *S. plusiae*, but restricted in known range to California and Arizona. *S. conata* is the only other species of this subgenus known north of Mexico; it is recorded from the San Francisco Bay area, Santa Cruz Island and San Bernardino Mtns. of California.

   As in *S. (Pseudosiphona)*, the greatest diversity of *S. (Siphonopsis)* species is in the Neotropics, particularly southern Mexico and southeastern Brazil (the latter area includes the type locality of the only described Neotropical species, *S. brasiliensis*). At least two species range from southern Mexico to southern Brazil. Several species are recognized from western South America from specimens collected in Colombia, Ecuador, Peru, and as far south as central Chile. Specimens have also been collected from Jamaica and Puerto Rico in the Caribbean.

List of described species included in *Siphona* (*Siphonopsis*)

S   *brasiliensis* (Townsend), 1929: 374 (*Siphonopsis*). Holotype female, Brazil: São Paulo (USNM). Holotype examined.

N   *conata* (Reinhard), 1959: 162 (*Siphonopsis*). Holotype male, USA: California, Marin Co., Mill Valley (CAS). Holotype examined.

N   *plusiae* Coquillett, 1895a: 125. Lectotype male (by designation of Coquillett, 1897: 76), USA: California (USNM). Lectotype examined.

List of examined, undescribed, species included in New World *Siphona* (*Siphonopsis*)

S. (Siphonopsis) sp. A: Males and females ranging from Oregon, USA, to northern Mexico (CAS, CNC, JEOH, MSU, PHA, UCB, UCD, UCR, UKL, USNM, WSUP). [Specimens of this "species" are noticeably and consistently different from those of *S. plusiae*, but have been frequently collected along with the latter - including at aggregation sites - so may represent variants of *S. plusiae*.]

S. (Siphonopsis) sp. B: Males and females ranging from Durango to Chiapas, Mexico (CNC).

S. (Siphonopsis) sp. C: Males from Chiapas, Mexico (CNC).

S. (Siphonopsis) sp. D: One male from Chiapas, Mexico (CNC).

S. (Siphonopsis) sp. E: Males and females from SE Brazil (BMNH, CAS, CNC, USP). Males from southern Mexico, Guatemala and Costa Rica are possibly conspecific (CNC, MSU, UCB, USNM).

S. (Siphonopsis) sp. F: One male from Veracruz, Mexico (CNC).

S. (Siphonopsis) sp. G: Two males from Ecuador (CNC).

S. (Siphonopsis) sp. H: Two males from Peru (CNC).

S. (Siphonopsis) sp. I: One male from Peru (CNC).

[No *S. (Siphonopsis)* sp. J.]

S. (Siphonopsis) sp. K: Males from southern Mexico and SE Brazil (BMNH, CNC, UCB, USP).

S. (Siphonopsis) sp. L: Males from SE Brazil (CNC).

S. (Siphonopsis) sp. M: Males and females from Brazil (CAS, CNC, USP) and Argentina (BMNH), and possibly Ecuador (CNC) and Peru (AMNH, USNM).

S. (Siphonopsis) sp. N: One male from Ecuador, males and two females from Chile (CNC).

Unstudied material includes specimens from the Caribbean: Puerto Rico (USNM) and Jamaica (USNM).

<div style="text-align:center">

Siphona (subgenus *Uruactia* Townsend)

Figs. 68, 99, 131.

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Uruactia Townsend, 1927: 256. Type-species, *U. uruhuasi* Townsend, 1927 (original designation). **New subgeneric status** in *Siphona* Meigen.

Recognition

This taxon of one described and one undescribed species is known only from three male specimens collected in Ecuador and Peru. Adults are relatively large, 4.0-5.0mm in length, with mostly yellow legs, rather dark thoracic dorsum, wings slightly darkened, abdomen yellow laterally on T_{1+2} and T_3 and rest reddish brown, and sparse abdominal pruinosity. The prementum is about half head height in length, and labella are padlike. These external features help in the recognition of *S. (Uruactia)* species, but examination of the male genitalia is necessary for a positive

identification.

The distiphallus of *S. (Uruactia)* species is the most distinctive feature of this taxon. It is smoothly tapered in profile, and with (Fig. 131) or without apical spines. It is similar in appearance to the distiphallus of *S. (Aphantorhapha)* species, but these taxa differ in other genitalic features and externally (*cf*. Recognition sections). Other male genitalic states of *S. (Uruactia)* species include the flattened median lobe of sternum 5 (Fig. 68), bare pregonite (Fig. 99), and inflexed cerci. These states complement the characteristic shape of the distiphallus and help to distinguish members of this taxon from other *Siphona s.l.* species.

The two known species of *S. (Uruactia)* are distinguished from one another by number of postsutural dorsocentral setae, setulation on wing vein R_{4+5}, relative development of lateral marginal setae on abdominal T_{1+2}, and slight differences in male genitalia (as indicated in description below).

Description
Length: 4.0-5.0mm.

Head.— Proclinate orbital setae subequal in length or anterior one longer. Eye of male medium-large, 0.84 head height (same size in all three examined specimens). Flagellomere 1 of male medium-short to medium, 0.48-0.50 head height; shape average (sp. 31) or broad (*S. uruhuasi*). Aristomere 1 short. Aristomere two 2X longer than wide. Aristomere 3 long and evenly tapered, micropubescent. Clypeus narrow and enclosed in membrane or slightly broadened. Palpus short, clavate. Proboscis with prementum medium in length, slightly longer than half head height, labella padlike.

Thorax.— Prosternum setulose. Lower katepisternal seta longer than upper anterior seta. Three (*S. uruhuasi*) or four (sp. 31) postsutural dorsocentral setae. Upper part of anepisternum with one or two setulae. Fore tibia with preapical *ad* seta much shorter than *d* seta. Mid tibia with one *ad* seta. Claws short. Wing vein CuA_1 with distal portion 0.26-0.46 (mean 0.36). Wing setulae: R_1 distally setulose dorsally, ventrally bare; R_{4+5} setulose between base and *r-m* in sp. 31, beyond *r-m* in *S. uruhuasi*; CuA_1 bare.

Abdominal terga 1-5.— Abdomen ovoid in shape. T_{1+2} without median marginal setae, lateral marginal setae absent from *S. uruhuasi*, strong in sp. 31. T_3-T_5 with average setation.

Male genitalia (Figs. 68, 99, 131).— S_5 (Fig. 68) with posterior margins of processes approximately U-shaped; apical lobe distinctly differentiated; median lobe flattened posteromedially, more prominently so in sp. 31 (Fig. 68); processes moderately setulose; T_6 apparently absent. Ejaculatory apodeme with fan-shaped portion subequal in width to width of hypandrial apodeme. Pregonite in profile apically pointed, smoothly curved anteriorly in *S. uruhuasi*, only slightly curved anteriorly in sp. 31 (Fig. 99); bare. Epiphallus absent. Distiphallus reduced posteriorly, entire laterally in *S. uruhuasi*, slightly incised laterally with short posterolateral arm in sp. 31 (Fig. 131), in profile rather narrow and apically pointed, apical margin with small (*S. uruhuasi*) to large (sp. 31) spines. Postgonite average. Surstylus long and straight, basally free from epandrium. Cerci average length, in profile sharply inflexed at midlength; moderately setose on basal half.

Examined male genitalia of: *S. uruhuasi* and sp. 31.

Female genitalia.— Not examined.

Hosts.   Unknown.

Phylogenetics
The two species are interpreted as sister species on the basis of shared states in the male genitalia (particularly shape of median lobes on sternum 5 and shape of distiphallus) and concordant external similarities. This taxon is retained as a

subgenus because its sister group within *Siphona s.l.* is unknown.

Geographic distribution

The type species of *S. (Uruactia)* is known only from the male holotype, collected from Uruhuasi, Peru, on 3.II.1910, at an elevation of 1980m, on flowers of *Baccharis* sp. The only other species, sp. 31 (originally numbered in series of unplaced New World *Siphona s.l.*), is represented by two male specimens, one with the same label data as the type of *S. uruhuasi* (USNM) and the other collected from Cerro Tinajillas in the Azuay province of southern Ecuador (18-21.III.1965 at 3100m; CNC).

List of described species included in *Siphona* (*Uruactia*)

S   *uruhuasi* (Townsend), 1927: 364 (*Uruactia*). Holotype male, Peru: Uruhuasi (USNM). Holotype examined.

List of examined, undescribed, species included in *Siphona* (*Uruactia*)

S. (Uruactia) sp. 31: One male each from Peru (USNM) and Ecuador (CNC).

New and described New World species unplaced to subgenus in *Siphona s.l.*
New World *Siphona* species group 1
Figs. 69, 100-101, 132.

This group of approximately nine known species (all undescribed) is Neotropical in distribution, ranging from southern Mexico to southeastern Brazil. They are typical members of *Siphona s.l.*, with no external features interpretable as synapotypic of the group. They include spp. 19,21,24-30[3], and are diagnosed as follows (also see Table 1): male eye medium-small to medium-large; male flagellomere 1 medium-short to medium-long, markedly varied in shape from linear or broadened to very broad and subquadrangular or almost triangular; aristomere 1 as long as wide in spp. 26 and 27, short in others; proboscis with labella varied from padlike (a few species) to almost length of prementum (most species), flexible in life on apical half or more; three or four postsutural dorsocentral setae; lower katepisternal seta longer than upper anterior seta; postscutellum unusually narrow and projected in spp. 29 and 30; R_1 and R_{4+5} with setulation varied, CuA_1 bare; crossvein *dm-cu* near wing margin in most species, moderately removed from it in a few.

Male genitalia of all nine species examined. Similarities in male genitalic features (particularly of the distiphallus) suggest monophyly of the group. S_5 (Fig. 69) with posterior margins of processes approximately U-shaped; apical lobe

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[3]Numbering of species is explained in Methods chapter.

distinctly differentiated, apex curved inward in a few species; median lobe markedly varied from narrow to elongate, rounded to truncate, or rather flattened posteromedially; slightly differentiated accessory lobe in sp. 27, others without. Pregonite (Figs. 100-101) in profile slender to average width, apically rounded to pointed; patch of small spines on apical half or less of sclerotized portion in most species (Fig. 100), spines absent from others (Fig. 101), tiny to moderate-sized seta posteriorly in a few species (absent from most). Epiphallus absent. Distiphallus (Fig. 132) relatively distinctive, not incised laterally, without enlarged teeth, in profile nearly parallel-sided on apical half or more and truncate apically. Postgonite markedly reduced in most species, average in a few. Surstylus varied from short to long, narrow to broad, straight to curved posteriorly; basally free from epandrium. Cerci thick on apical half in sp. 21, average in others, smoothly curved at midlength.

Female genitalia (examined in spp. 24,27,30) short, unmodified except sternum 8 broader than average in sp. 30.

List of examined, undescribed, species included in New World *Siphona* species group 1

Siphona species group 1, sp. 19: One male from Chiapas, Mexico (CNC).
Siphona species group 1, sp. 21: Males and females from SE Brazil, one male from Colombia (CNC).
Siphona species group 1, sp. 24: Males and females from northern Argentina (CNC), one male from Ecuador (USNM).
Siphona species group 1, sp. 25: One male from northern Argentina (CNC).
Siphona species group 1, sp. 26: Males from Ecuador (BMNH, CNC).
Siphona species group 1, sp. 27: One male and one female from Ecuador (CNC).
Siphona species group 1, sp. 28: One male from Chiapas, Mexico (CNC), possibly conspecific males from Guatemala (USNM) and Costa Rica (USNM).
Siphona species group 1, sp. 29: Males and one female from Ecuador (CNC).
Siphona species group 1, sp. 30: Males and females from Ecuador (CNC).

New World *Siphona* species group 2
Figs. 19, 70, 102-103, 133-134.

This group comprises about ten species[4] distributed between southern Arizona and southeastern Brazil. They are typical members of *Siphona s.l.*, with the following characteristics (also see Table 1): (head of sp. 1 shown in Fig. 19) male eye medium-large to large; male flagellomere 1 medium-short to medium, linear to subquadrangular in shape; aristomere 1 short; proboscis with labella about two-thirds length of prementum in sp. 8, padlike in others; three postsutural dorsocentral setae; lower katepisternal seta longer than upper anterior seta; wing setulation varied; crossvein *dm-cu* slightly removed from wing margin in most species.

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[4]These species are numbered from one to ten, separately from those of species groups 1 and 3 and unplaced New World species, as explained in Methods chapter.

Male genitalia of all ten included species examined. S_5 (Fig. 70) with posterior margins of processes approximately U-shaped; apical lobe distinctly differentiated, apex curved inward in a few species; median lobe markedly varied from broadly rounded to elongate, and truncate or flattened posteromedially, with accessory lobe distinctly differentiated in a few species. Pregonite (Figs. 102-103) varied in profile, smoothly to sharply curved anteriorly, average to broad on basal half; with or without patch of small spines on apical half or less of sclerotized portion and in sp. 2 (Fig. 103) with longitudinal row of spines, bare posteriorly or with tiny to moderate-sized seta. Epiphallus absent. Most included species are recognized as members of this species group by features of the distiphallus: most possess posterolaterally on each side a ventrally or anteroventrally directed projection or hook (Figs. 133-134); a few species lack this feature of the distiphallus but are included in this species group (with varied degrees of confidence) because of other external and genitalic similarities; posterior margin of distiphallus entire in sp. 2, incised in others. Postgonite markedly reduced in spp. 3 and 10, short in sp. 2, average in others. Surstylus average length to elongate, straight to curved posteriorly; basally free from epandrium. Cerci rather short to average length, straight to smoothly curved.

Female genitalia (examined in spp. 3 and 6) short, unmodified except sternum 8 broader than average.

The conservative external features of members of *Siphona* species group 2 make this group difficult to recognize. In addition certain species are less apotypic than most in their male genitalic features, so their inclusion here is tentative and is based on general similarities.

List of examined, undescribed, species included in New World *Siphona* species group 2

Siphona species group 2, sp. 1: Males and females ranging from southern Arizona, USA, to Chiapas, Mexico (CAS, CNC, UAT).
Siphona species group 2, sp. 2: One male from Michoacan, Mexico (USNM).
Siphona species group 2, sp. 3: Males and females from Chiapas, Mexico (CNC).
Siphona species group 2, sp. 4: One male from Chiapas, Mexico (CNC).
Siphona species group 2, sp. 5: One male from Panama (USNM), males and one female from Peru (CNC).
Siphona species group 2, sp. 6: Males and females from SE Brazil (CNC, INPA, USP).
Siphona species group 2, sp. 7: Males from Peru (CNC).
Siphona species group 2, sp. 8: Males from Peru (CNC).
Siphona species group 2, sp. 9: One male from Costa Rica (USNM).
Siphona species group 2, sp. 10: One male from Chiapas, Mexico (CNC).

New World *Siphona* species group 3
Figs. 104-105, 135.

Five undescribed New World species are recognized as belonging to a monophyletic lineage possibly related to *Siphona* species group 1 (see below).

Included are spp. 3, 4, 6, 12 and 22 (SE Brazil)[5]. Externally these flies are quite varied, particularly in head features and wing setulation, and for this reason specimens of some of these species appear more externally similar to excluded species than to their own group members. As a rule, male genitalic characteristics are more reliable indicators of relationship within *Siphona s.l.* than are external features (species of *S. (Pseudosiphona)* and *S. (Siphonopsis)* being good examples), so little weight is given here to such homoplastic external similarities.

Siphona species group 3 is diagnosed as follows (also see Table 1): male eye medium to medium-large; male flagellomere 1 markedly varied, medium-short to long; shape linear to very broadly triangular; proboscis with labella slightly lengthened in some specimens of sp. 22, padlike in others; three postsutural dorsocentral setae; varied wing setulation; position of crossvein *dm-cu* varied; legs and abdomen average; (male genitalia examined in all five species) sternum 5 with posterior margins of processes approximately U-shaped, apical lobe not apically curved inward, median lobe rounded to elongate and truncate, distinctly differentiated accessory lobes in sp. 4; pregonite (Figs. 104-105) in profile rather sharply curved at midlength or smoothly curved anteriorly, with longitudinal ridge of spines laterally (resembling pregonite of *Entomophaga* and *Proceromyia* except possessing tiny to moderate-sized seta posteriorly in most specimens [*i.e.* of two examined specimens of sp. 22, one has tiny seta and the other is bare, Fig. 105] - this seta only present among *Siphona* group taxa); pregonite without group of small spines apically; epiphallus absent; distiphallus (Fig. 135) not incised laterally, characteristically squared-off basally, with short, parallel-sided apical portion ending in truncate tip, moderately developed spines anteriorly in sp. 22, only spinules present in others; postgonite average to reduced; surstylus and cerci average; female genitalia short and unmodified (examined only in sp. 3).

Two members of *Siphona* species group 1 (spp. 26 and 27) have similar distiphallus structure to species of group 3, but differ in features of the pregonite. Species of group 3 possess a spined longitudinal ridge on the outer surface of the pregonite, a state not found in other species of *Siphona s.l.* except in *Siphona* sp. grp. 2, sp. 2 (Fig. 103). There are both external similarities and dissimilarities between members of both groups 1 and 3, but these involve such homoplastic characters that their phylogenetic interpretation is difficult. I have not studied the groups in sufficient detail to offer any definite views about the interrelationships of groups 1 and 3, but I suggest that certain male genitalic similarities may indicate that the species of group 3 are derived members of group 1 or the groups are sister groups.

I have presented the information above about *Siphona* group 3, as I have elsewhere for groups 1 and 2, to provide a tentative framework upon which a formal taxonomic investigation of the numerous undescribed and unplaced New World

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[5] Numbering of these species is explained in Methods chapter.

Siphona s.l. species can be built. These notes about undescribed New World siphonines ought to prove useful in the eventual revision of this large and unworked assemblage of *Siphona* species.

List of examined, undescribed, species included in New World *Siphona* species group 3

Siphona species group 3, sp. 3: Males and females ranging from Washington state to southern California and Arizona, USA (CAS, CNC, PHA, UCB, UCR, USNM, WSUP).
Siphona species group 3, sp. 4: One male each from Veracruz and Chiapas, Mexico (CNC).
Siphona species group 3, sp. 6: One male from Florida, USA (AMNH), one possibly conspecific male from Chiapas, Mexico (USNM).
Siphona species group 3, sp. 12: Two males from Iowa, USA (PHA), one male from Ohio, USA (CNC) and one female from Ontario, Canada (CNC).
Siphona species group 3, sp. 22: Males from SE Brazil (CAS, CNC, USP).

Unplaced New World species of *Siphona sensu lato*
Figs. 20, 106, 136.

I have left two described species unplaced within New World *Siphona s.l.*: *Siphona panamensis* (Curran) and *Siphona pulla* (Reinhard). Though typical members of *Siphona s.l.*, these species cannot be associated with any of the subgenera here recognized nor the three additional species groups discussed. Both are difficult to place because they are only known from female holotypes, and if males were available then unequivical placement of these species might be possible.

Specimens of many undescribed species were examined during the course of this revision. Those belonging to relatively easily recognized genera are incorporated into the descriptions of those genera and not themselves described or specially treated. This practise is more difficult within *Siphona s.l.* because monophyletic lineages are difficult to recognize and many species cannot be associated with the lineages that are. The complexity is all the more difficult to discuss since most of the species are undescribed. As this work is primarily a generic level revision it is impractical at this time to describe these new species, though discussing them in an informal manner will convey some idea of their diversity. Where possible, descriptions of certain subgenera (particularly *S. (Pseudosiphona)* and *S. (Siphonopsis)*) have been modified for inclusion of appropriate undescribed species, but even though this has been done and *Siphona* groups 1 to 3 informally diagnosed, at least 15 undescribed New World species remain that I have studied but not been able to place. I outline below some of the diversity contained within this group of mostly unrelated species because they may remain undescribed for some time. As new groups or subgenera are erected for some of these species and other species identified as related to groups recognized here, the descriptions of the latter will have to be modified for such inclusions. For the present I have retained a rather conservative approach toward recognition of New World *Siphona* subgenera in order to keep them as monophyletic lineages (and thus, I believe, more meaningful

entities) in the midst of a plethora of undescribed forms.

The species discussed here include *S. panamensis, S. pulla,* and 15 numbered species: spp. 1,2,5,7,8,10,13-17,20,23,32 and 34[6]. Their range of variation is given in Table 1 under the heading of "*Siphona s.l.,* unplaced", and the assemblage is briefly diagnosed here: (head of sp. 23 shown in Fig. 20) male eye medium-small to very large; male flagellomere 1 short to medium, shape linear, broadened, subquadrangular or broad and triangular; proboscis with labella padlike in most species, slightly lengthened in a few, about as long as prementum in spp. 13 and 23 (Fig. 20); three postsutural dorsocentral setae in most species, four in a few; lower katepisternal seta longer than upper anterior seta in most species, subequal in length in a few, shorter in spp. 14 and 17; R_1 and R_{4+5} with setulation varied, CuA_1 bare; crossvein *dm-cu* positioned near or removed from wing margin; legs average.

Male genitalia of 14 species examined (spp. 1-2,5,7-8,10,13-17,23,32,34). S_5 with posterior margins of processes approximately U-shaped in most species, obtusely angled in a few, nearly V-shaped in spp. 7 and 15 (though median cleft more distinct than in *Actia* species); apical lobe distinctly differentiated, apex curved inward in some species; median lobe varied, rounded, elongate, truncate, or slightly flattened posteromedially, accessory lobe present in sp. 5; pregonite (Fig. 106) varied, in profile slender to broad, apically pointed to rounded, small spines on sclerotized portion apically in a few species, with tiny to moderate-sized seta posteriorly in most species, seta absent from a few. Epiphallus absent. Distiphallus (Fig. 136) markedly varied, laterally incised or complete, with or without enlarged spines apically, in profile varied apically from pointed or rounded to truncate. Postgonite average in most species, reduced in spp. 32 and 34. Surstylus and cerci average in most species, surstylus basally free from epandrium.

Female genitalia examined in seven species (spp. 1-2,5,10,14,20,23), short; S_6 sharply keeled posteromedially in sp. 20, flat in others; T_6 absent, or present as lateral sclerites or (in sp. 3) as a dorsally continuous sclerite; S_7 with rather short anterior apodeme in sp. 20, long in others, sharply keeled posteromedially only in sp. 20; S_8 average in most species, very broad in sp. 5, with thick setae in sp. 20.

The highest concentration of species (six) is in southern Mexico, with seven other species distributed throughout North America from Alaska to northcentral Mexico and four species distributed between southeastern Brazil and lower Central America.

Hosts are known only for New World species 7 and 8, and include larvae of several species of the Geometridae and one of the Noctuidae. Species 7 and 8 are recorded from southern British Columbia, Canada.

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[6] Numbering of these species is explained in Methods chapter.

List of described species unplaced to subgenus in New World *Siphona sensu lato:*

S   *Actia panamensis* Curran, 1933a: 3. Holotype female, Panama: Barro Colorado Is. (AMNH). Holotype examined. (Removed from *Actia*.)

N,S *Aphantorhapha pulla* Reinhard, 1974: 1157. Holotype female, Mexico: Morelos, Cuernavaca (CNC). Holotype examined. (Removed from *Aphantorhapha*.)

List of examined, undescribed, species unplaced in New World *Siphona sensu lato*

Unplaced *Siphona* sp. 1: Males and females from western North America (CNC, PHA, UCB, USNM, WSUP).

Unplaced *Siphona* sp. 2: Males and females ranging from Alaska to Wisconsin, USA (CNC, USNM).

Unplaced *Siphona* sp. 5: Males and females from southern Mexico (CNC), one male from El Salvador (USNM).

Unplaced *Siphona* sp. 7: Males and females from southern British Columbia, Canada, one male from California, USA, and one possibly conspecific male from Arizona, USA (CNC).

Unplaced *Siphona* sp. 8: Males and females from southern British Columbia, Canada (CNC).

Unplaced *Siphona* sp. 10: One male from Ontario, Canada (CNC) and one female from New Brunswick, Canada (JEOH).

Unplaced *Siphona* sp. 13: One male from Florida, USA (CNC).

Unplaced *Siphona* sp. 14: Males and females from Chiapas, Mexico (CNC).

Unplaced *Siphona* sp. 15: One male from Oaxaca, Mexico (JEOH).

Unplaced *Siphona* sp. 16: One male from Durango, Mexico (CNC).

Unplaced *Siphona* sp. 17: One male from Chiapas, Mexico (CNC).

Unplaced *Siphona* sp. 20: One female from Chiapas, Mexico (CNC).

Unplaced *Siphona* sp. 23: Males and females from SE Brazil, Ecuador, Costa Rica and Canal Zone (AMNH, BMNH, CNC, USNM, USP).

Unplaced *Siphona* sp. 32: Males from SE Brazil (USP).

Unplaced *Siphona* sp. 34: Males and females from SE Brazil (CNC, USNM, USP), one male from Ecuador (CNC) and one female from Costa Rica (USNM).

Actia heterochaeta Bezzi, unplaced species of the Siphonini

I have been unable to locate the female type of this species, described from Ethiopia by Bezzi (1908: 59). The type apparently does not reside in Milan (MCSN) with many of the other Bezzi types (Arnaud 1982).

Actia heterochaeta was described by Bezzi under a concept of *Actia* now equivalent to the entire Siphonini. The original description fails to mention a single generic characteristic that would help in the placement of this species. Bezzi compares *A. heterochaeta* with *A. bicolor* (now in *Ceromya*) in his original description, and then with *A. stiglinae* (now in *Peribaea*) in a later publication (1928: 204). It is clear that Bezzi's concept of "allied species" was based on shared similarities and not commonality of descent, so his species comparisons provide no clue about the correct placement of *A. heterochaeta*.

I examined a male specimen in the BMNH collected from Nigeria and identified by Villeneuve as *A. heterochaeta*. This specimen is probably the one mentioned by Crosskey (1980: 855) as a questionable new locality record for the species. However, Villeneuve's identification is probably in error because the specimen (a *Peribaea* species) differs from the description of *A. heterochaeta* in two important respects: R_1 is bare in *A. heterochaeta* and distally setulose in Villeneuve's specimen, and coloration differs markedly (even given that Bezzi's specimen was a female and Villeneuve's specimen a male). Without any concrete indication of the generic characteristics of *A. heterochaeta*, I must leave this species unplaced in the Siphonini, as did Crosskey (1980: 855).
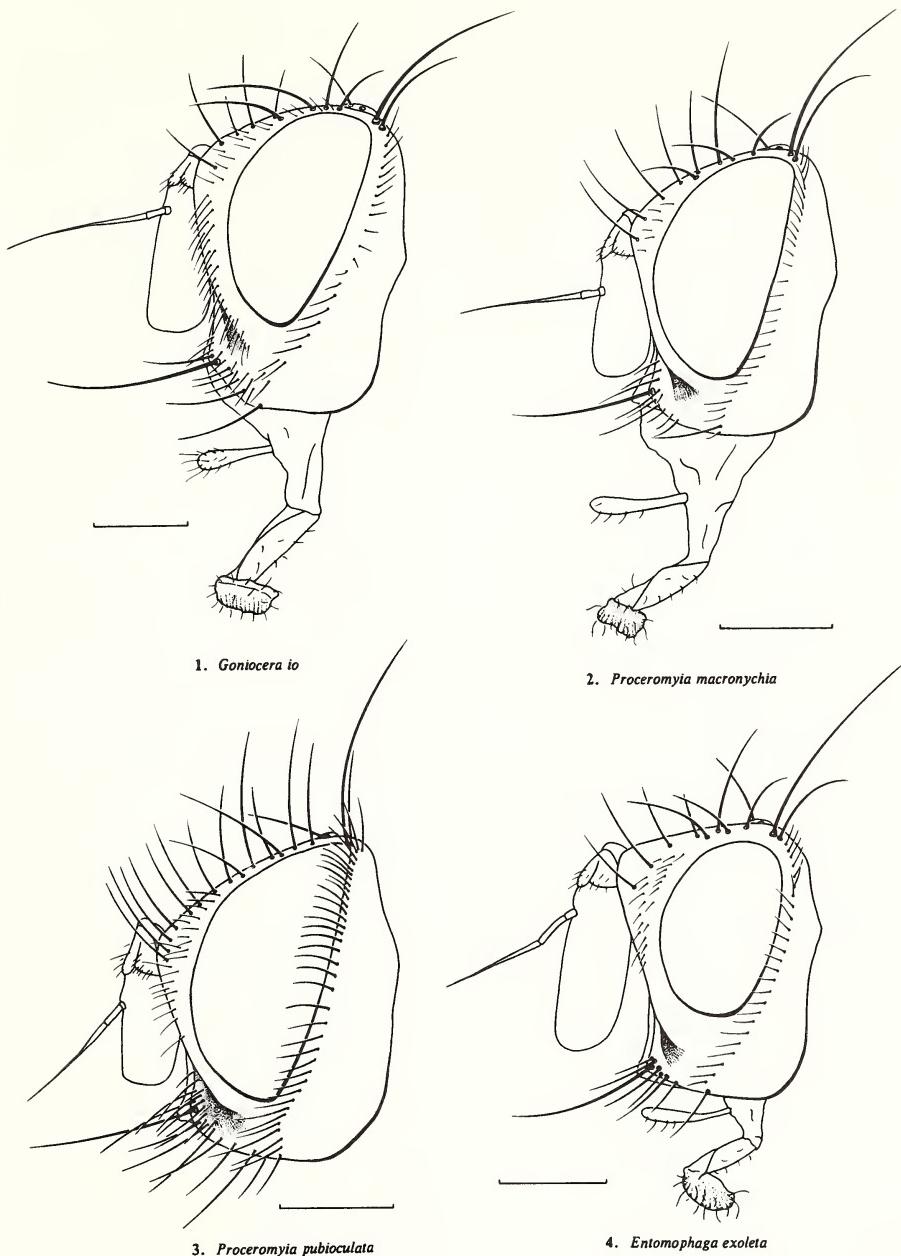
Figs. 1–4. Head profiles of male siphonines (vestiture of postcranium omitted). Scale bars = 0.5mm: 1, *Goniocera io*; 2, *Proceromyia macronychia*; 3, *Proceromyia pubioculata*; 4, *Entomophaga exoleta*.
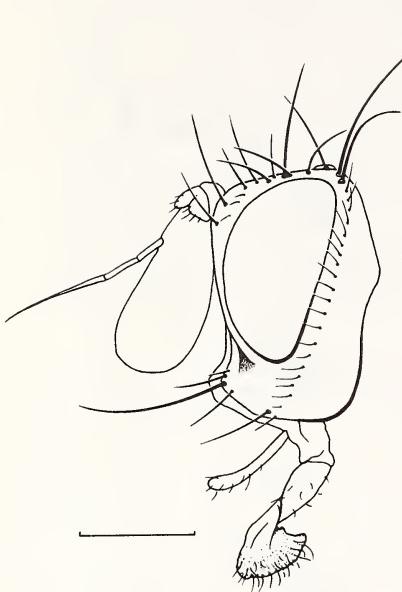
5. *Entomophaga nigrohalterata*
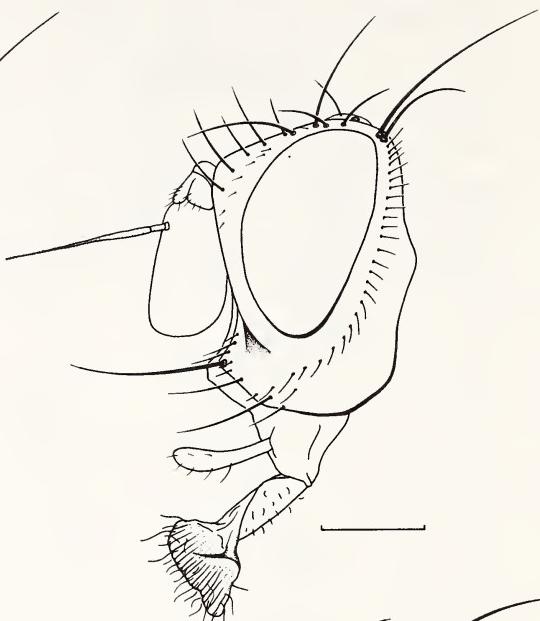
6. *Ceromya flaviceps*
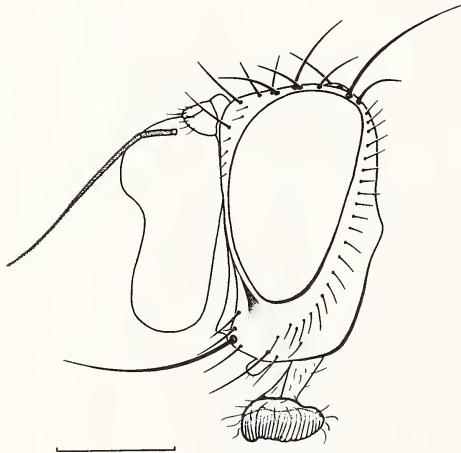
7. *Ceromya* New Guinea sp. 15
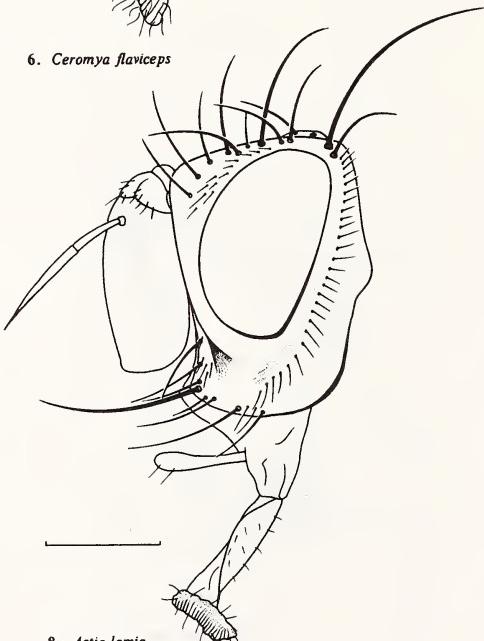
8. *Actia lamia*

Figs. 5–8. Head profiles of male siphonines (vestiture of postcranium omitted). Scale bars = 0.5mm: 5, *Entomophaga nigrohalterata*; 6, *Ceromya flaviceps*; 7, *Ceromya* New Guinea sp. 15; 8, *Actia lamia*.
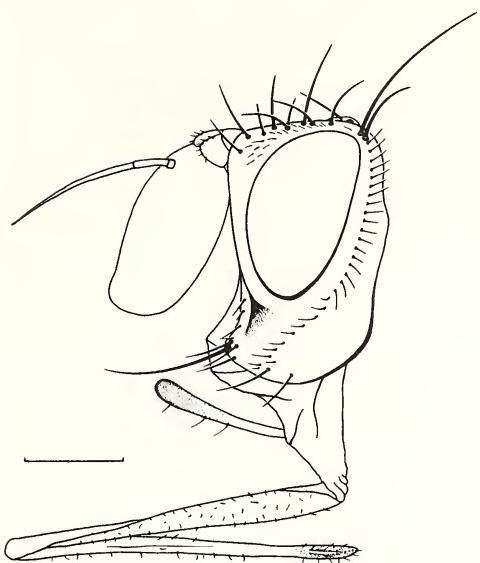
9. *Actia* Nepal sp. 1
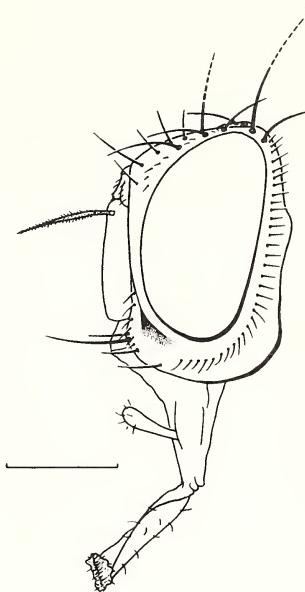
10. *Actia parviseta*
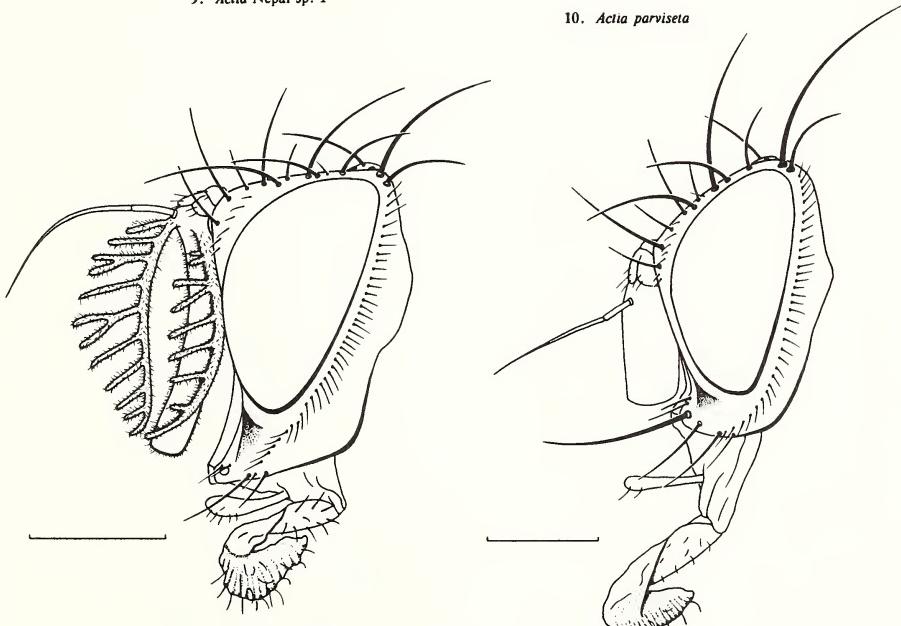
11. *Peribaea cervina*
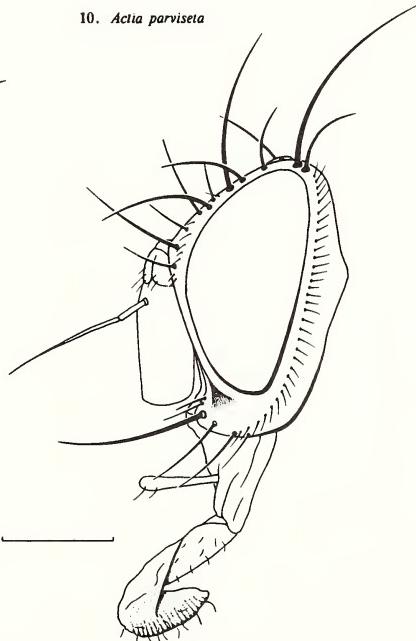
12. *Peribaea tibialis*

Figs. 9–12. Head profiles of male siphonines (vestiture of postcranium omitted). Scale bars = 0.5mm: 9, *Actia* Nepal sp. 1; 10, *Actia parviseta* (from holotype, proboscis reoriented); 11, *Peribaea cervina* (from holotype, vibrissae missing); 12, *Peribaea tibialis*.
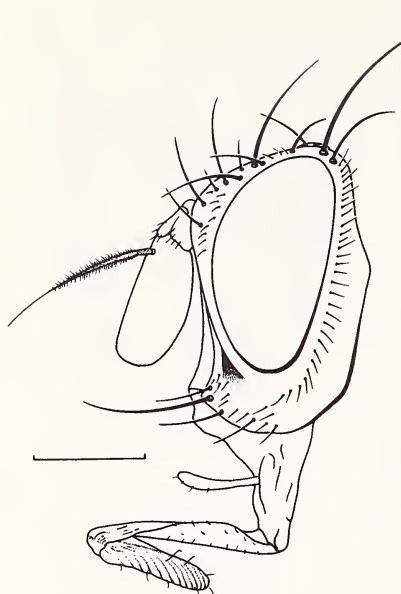
13. *S. (Actinocrocuta) singularis* complex
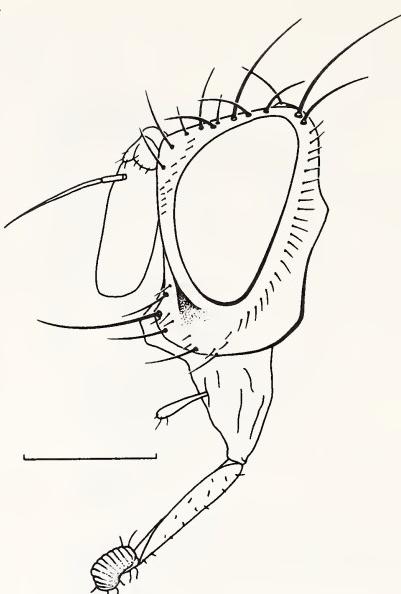
14. *S. (Aphantorhapha) arizonica*
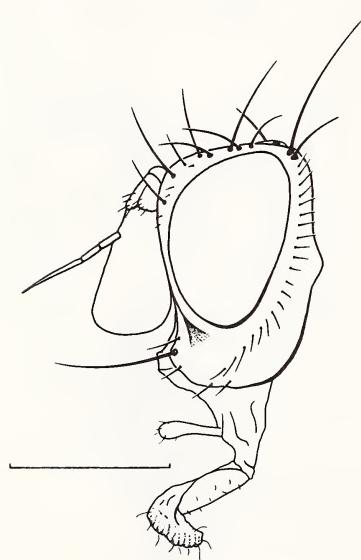
15. *S. (Baeomyia) xanthogaster*
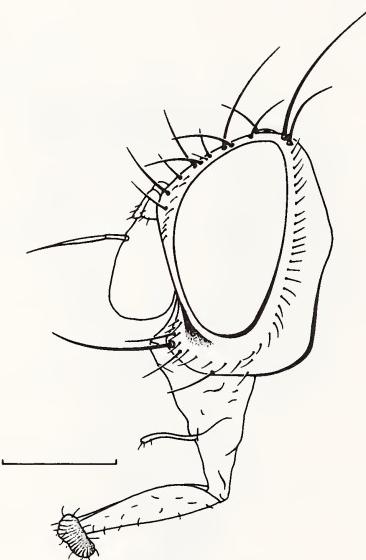
16. *S. (Ceranthia) flavipes*

Figs. 13–16. Head profiles of male siphonines (vestiture of postcranium omitted). Scale bars = 0.5mm: 13, *Siphona (Actinocrocuta) singularis* complex; 14, *Siphona (Aphantorhapha) arizonica*; 15, *Siphona (Baeomyia) xanthogaster* (from holotype); 16, *Siphona (Ceranthia) flavipes*.
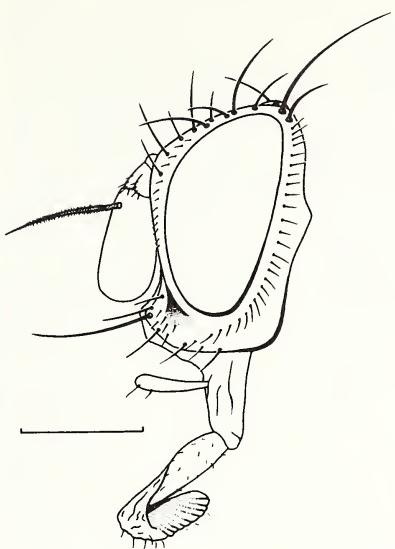
17. *S. (Pseudosiphona) brevirostris*
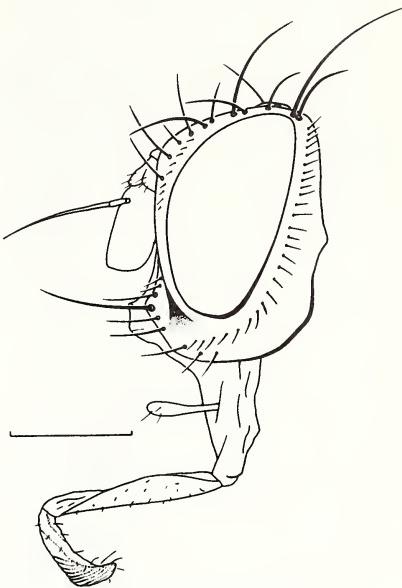
18. *S. (Siphonopsis) plusiae*
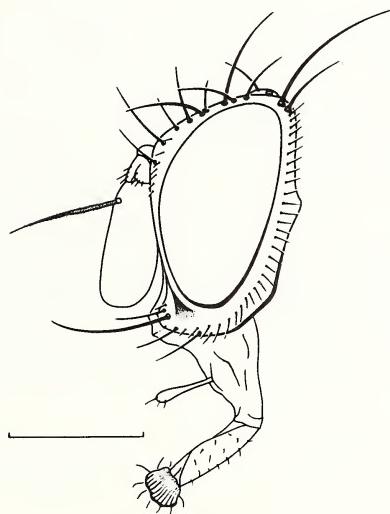
19. *Siphona s.l.*, sp. grp. 2, sp. 1
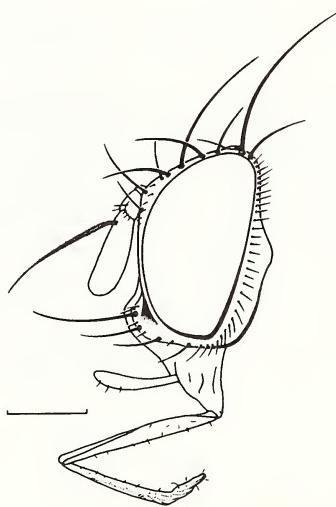
20. *Siphona s.l.*, unplaced sp. 23

Figs. 17–20. Head profiles of male siphonines (vestiture of postcranium omitted). Scale bars = 0.5mm: 17, *Siphona (Pseudosiphona) brevirostris*; 18, *Siphona (Siphonopsis) plusiae*; 19, *Siphona s.l.*, sp. grp. 2, sp. 1; 20, *Siphona s.l.*, unplaced sp. 23.
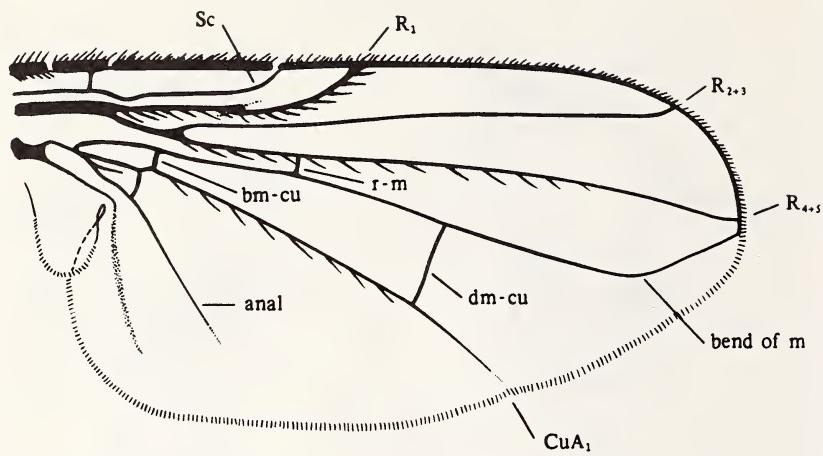
21. *Actia interrupta*
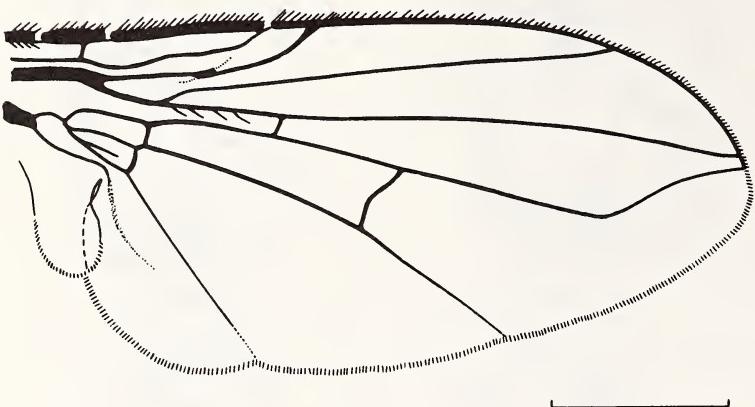
22. *S. (Baeomyia) xanthogaster*

Figs. 21–22. Right wings of siphonines. Scale bars = 0.5mm: 21, *Actia interrupta*, with wing veins labelled; 22, *Siphona (Baeomyia) xanthogaster*.
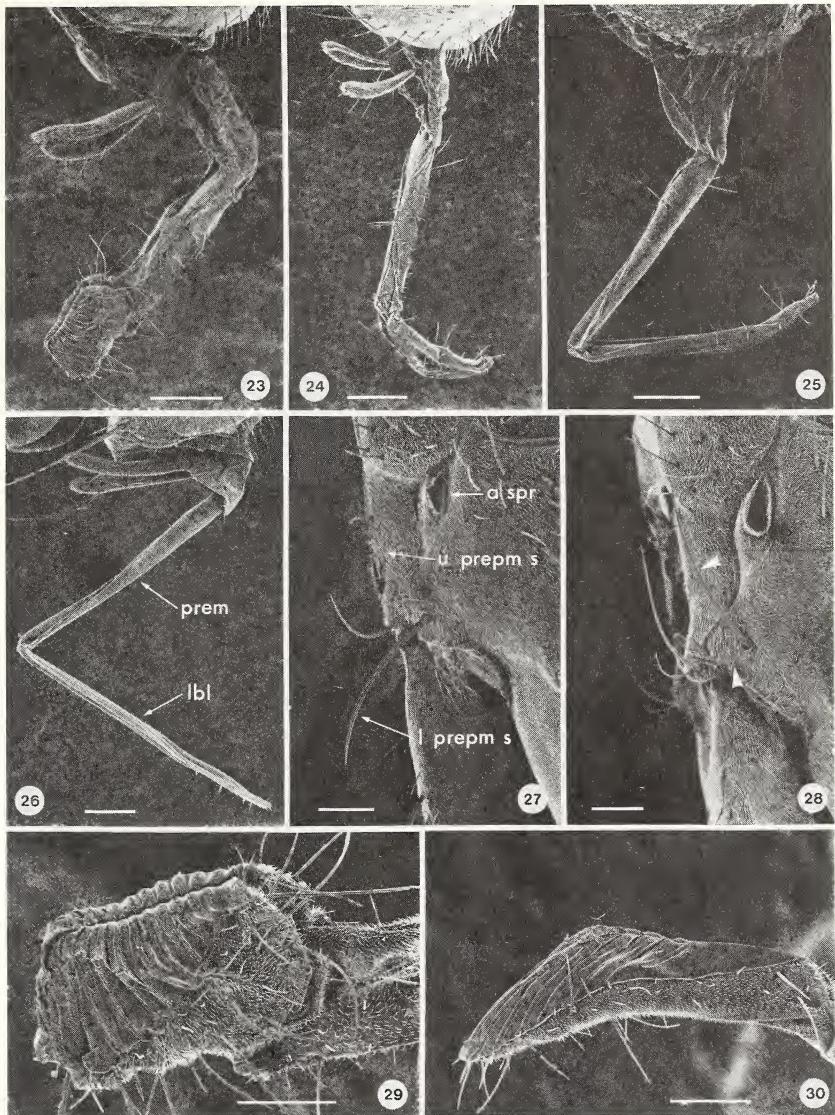
Figs. 23–26. Comparison of proboscis structure. Scale bars = 200μm: 23, *Actia diffidens*, with padlike labella; 24, *Siphona (Siphonopsis) plusiae*, with elongate labella; 25, *Siphona (Siphona) maculata*, with long labella; 26, *Siphona (Siphona) pisinnia*, with very long labella (*lbl*, labella; *prem*, prementum). Figs. 27–28. Left lateral view of prothorax, for comparison of proepimeral setae. Scale bars = 100μm: 27, *Peribaea* sp., illustrating two strong and opposed proepimeral setae (*a spr*, anterior spiracle; *l prepm s*, lower proepimeral seta; *u prepm s*, upper proepimeral seta); 28, *Siphona (Siphona) maculata*, illustrating single strong proepimeral seta (upper and lower setae indicated by arrows). Figs. 29–30. Comparison of labella of proboscis. Scale bars = 100μm: 29, labella of *Actia diffidens*, illustrating padlike condition and numerous pseudotracheae; 30, labella of *Siphona (Siphonopsis) plusiae*, illustrating elongate condition and relatively few pseudotracheae.
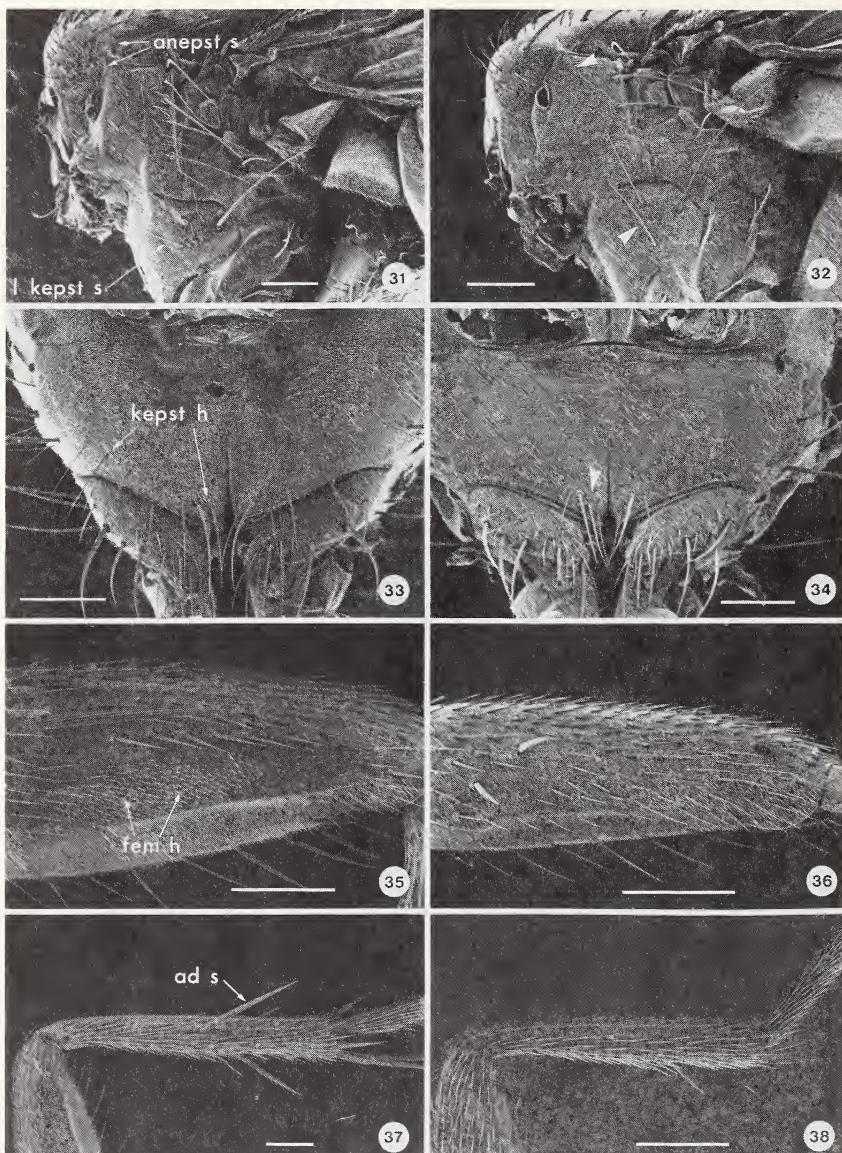
Figs. 31–32. Left lateral view of thorax, for comparison of katepisternal and anepisternal setae. Scale bars = 250µm: 31, *Actia diffidens*, illustrating short lower katepisternal seta (*l kepst s*) and two anepisternal setulae (*anepst s*); 32, *Siphona (Siphona) maculata*, illustrating long lower katepisternal seta and single anepisternal setula (indicated by arrows). Figs. 33–34. Ventral view of mesothorax, for comparison of posteroventral region of katepisternum. Scale bars = 200µm: 33, *Actia diffidens*, illustrating row of hairs on katepisternum (*kepst h*) anterior to mid coxa; 34, *Siphona (Siphona) maculata*, illustrating presence of several hairs on katepisternum restricted to midline region (indicated by arrow). Figs. 35–36. Comparison of anterior surface of mid femur. Scale bars = 200µm: 35, *Ceromya varichaeta*, illustrating patch of tiny hairs on anterior surface of mid femur (*fem h*); 36, *Siphona (Siphona) maculata*, illustrating typical condition of anterior surface of mid femur. Figs. 37–38. Comparison of anterior surface of mid tibia. Scale bars = 200µm: 37, *Ceromya varichaeta*, illustrating presence of strong anterodorsal seta (*ad s*) on mid tibia; 38, *Siphona (Baeomyia) xanthogaster*, illustrating absence of anterodorsal seta on mid tibia.
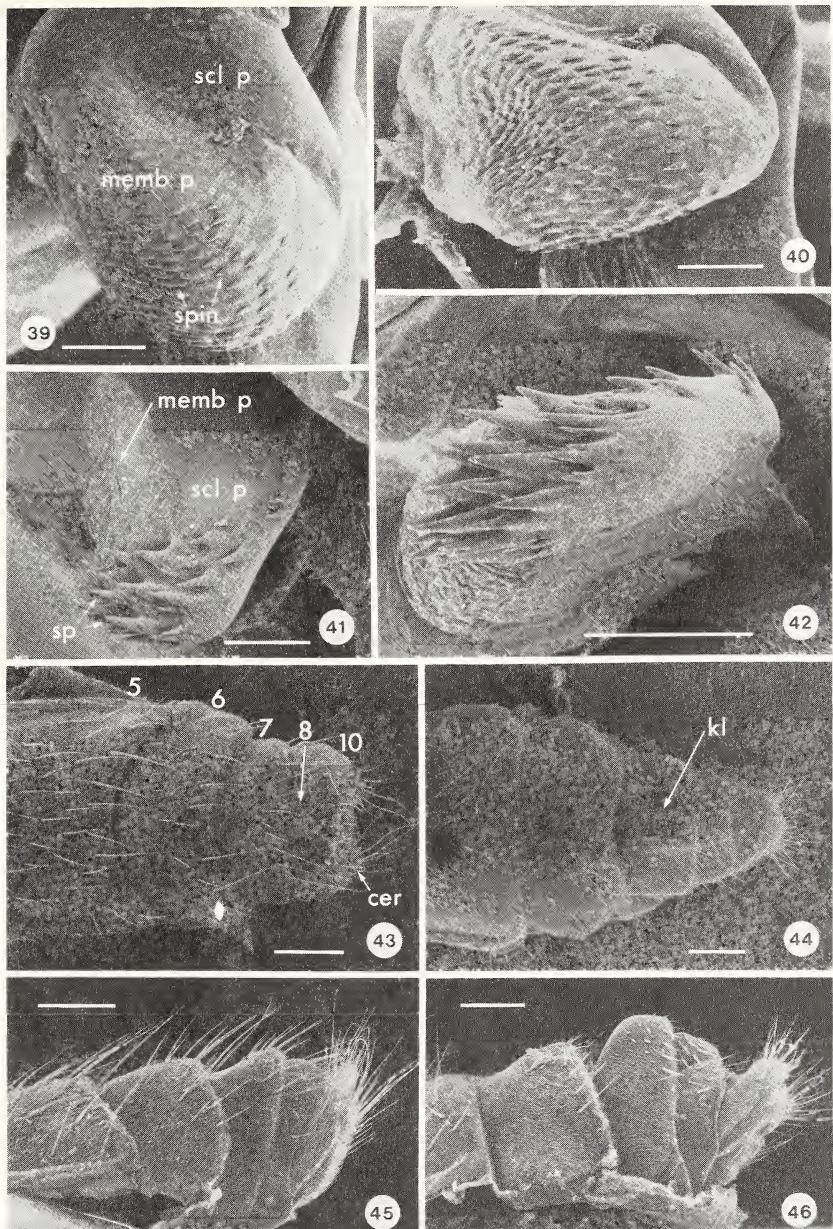
Figs. 39–42. Comparison of male pregonite structure. Scale bars = 40μm: 39, left lateral view of pregonite of *Ceromya americana* complex, illustrating spinules on membranous portion (*memb p*, membranous portion; *scl p*, sclerotized portion; *spin*, spinules); 40, ventrolateral view of pregonite of *Ceromya americana* complex; 41, left lateral view of pregonite of *Actia diffidens*, illustrating large spines (*sp*) on sclerotized portion; 42, ventral view of pregonite of *Actia diffidens*. Figs. 43–46. Comparison of female genitalia. Scale bars = 100μm: 43, ventral view of female genitalia of *Siphona (Siphona) maculata*, illustrating unmodified sterna (sterna numbered; *cer*, cercus); 44, ventral view of female genitalia of *Siphona (Ceranthia) flavipes*, illustrating keel (*kl*) posteromedially on sternum 7; 45, lateral view of female genitalia of *Siphona (Siphona) maculata*; 46, lateral view of female genitalia of *Siphona (Ceranthia) flavipes*.
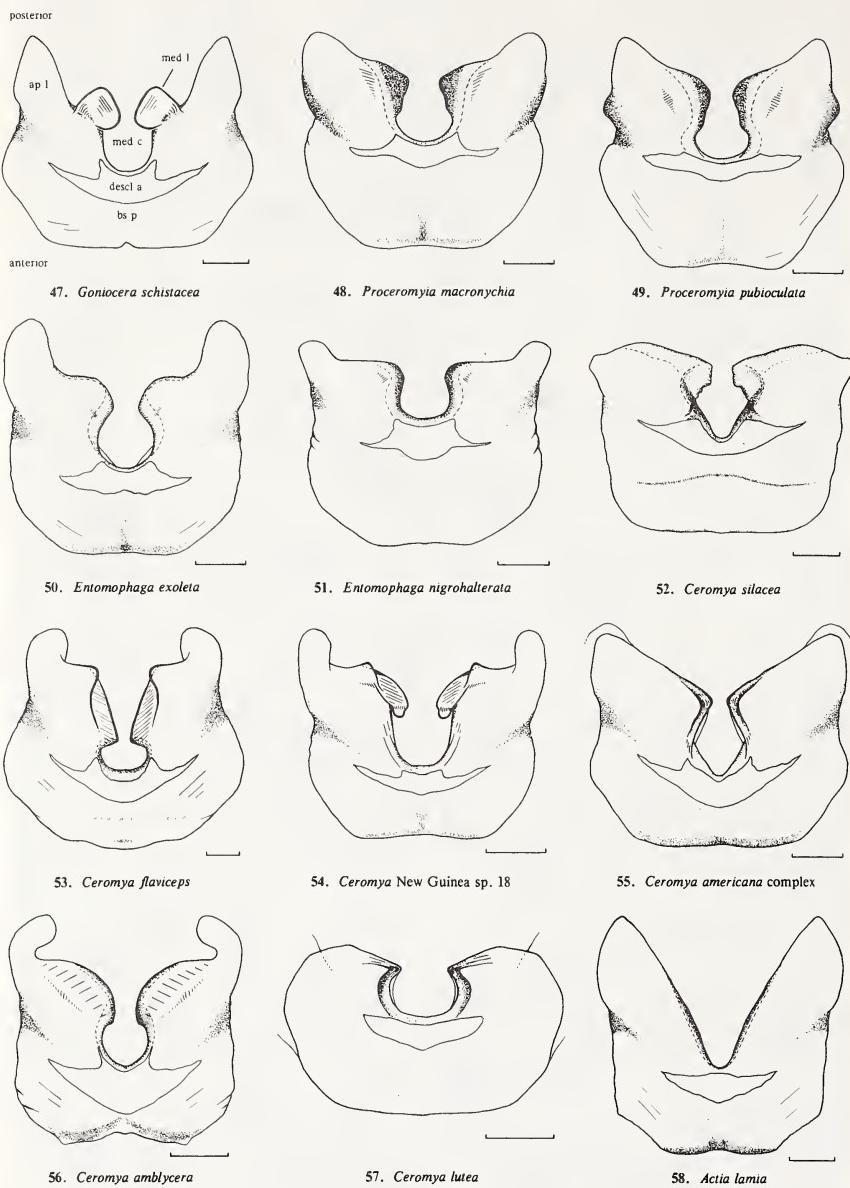
Figs. 47–58. Ventral view of male sternum 5. Scale bars = 0.1mm: 47, *Goniocera schistacea* (Y68, CNC) (*ap l*, apical lobe; *bs p*, basal plate; *descl a*, desclerotized area; *med c*, median cleft; *med l*, median lobe); 48, *Proceromyia macronychia* (Y40, CNC); 49, *Proceromyia pubioculata* (Y85, JEOH); 50, *Entomophaga exoleta* (Y132, ZMUC); 51, *Entomophaga nigrohalterata* (Y27, CNC); 52, *Ceromya silacea* (Y179, CNC); 53, *Ceromya flaviceps* (Y107, CNC); 54, *Ceromya* New Guinea sp. 18 (Y175, BLKU); 55, *Ceromya americana* complex (Y26, CNC); 56, *Ceromya amblycera* (Y45, UCS); 57, *Ceromya lutea* (Y121, CNC); 58, *Actia lamia* (Y17, JEOH).

59. *Actia autumnalis*

60. *Peribaea apicalis*

61. *Peribaea* Australia sp. 1

62. *S. (Actinocrocuta) singularis* complex

63. *S. (Aphantorhapha) arizonica*

64. *S. (Aphantorhaphopsis)* Nepal sp. 1

65. *S. (Ceranthia) flavipes*

66. *S. (Pseudosiphona)* sp. 4

67. *S. (Siphona) cristata*

68. *S. (Uruactia)* sp. 31

69. *Siphona s.l.*, sp. grp. 1, sp. 28

70. *Siphona s.l.*, sp. grp. 2, sp. 9
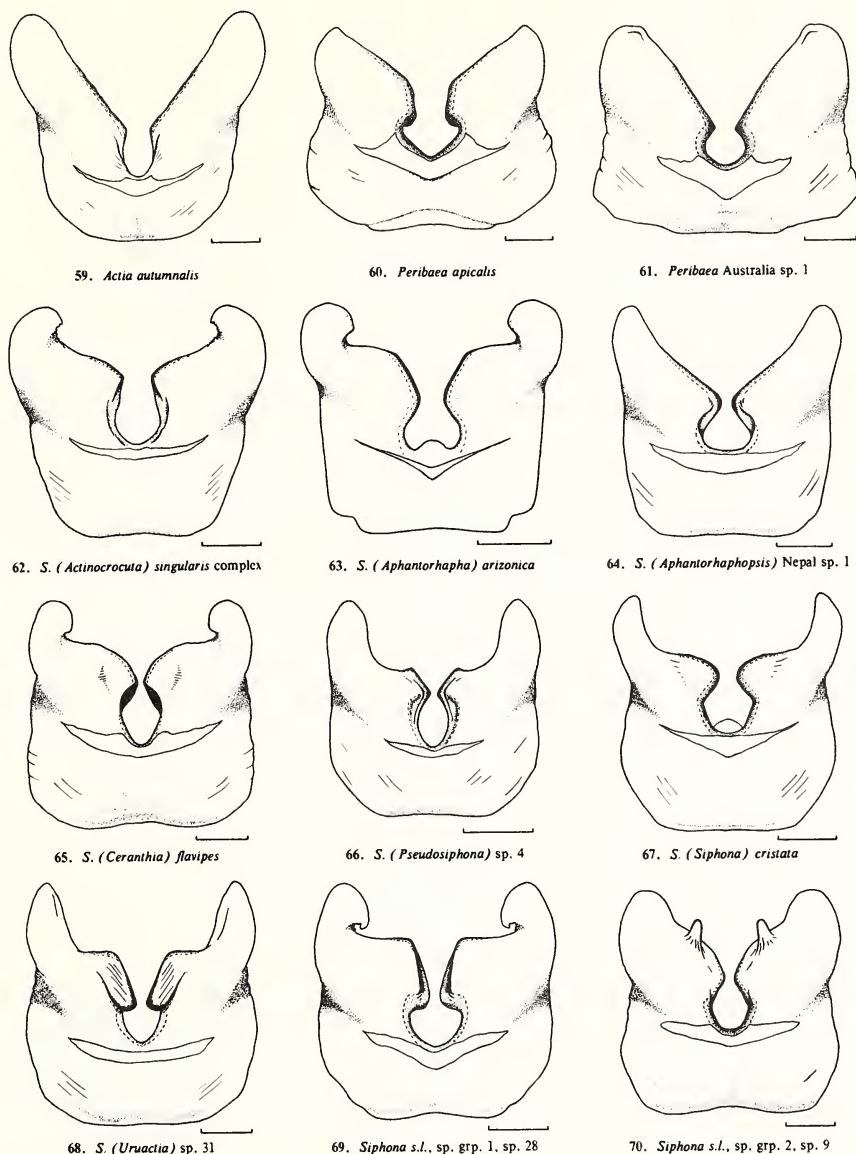
Figs. 59–70. Ventral view of male sternum 5. Scale bars = 0.1mm: 59, *Actia autumnalis* (Y22, CNC); 60, *Peribaea apicalis* (Y82, CNC); 61, *Peribaea* Australia sp. 1 (Y83, DPI); 62, *Siphona (Actinocrocuta) singularis* complex (O120, CNC); 63, *Siphona (Aphantorhapha) arizonica* (unnumbered, JEOH); 64, *Siphona (Aphantorhaphopsis)* Nepal sp. 1 (W75, CNC); 65, *Siphona (Ceranthia) flavipes* (B8, CNC); 66, *Siphona (Pseudosiphona)* sp. 4 (R22, CNC); 67, *Siphona (Siphona) cristata* (W38, JEOH); 68, *Siphona (Uruactia)* sp. 31 (R45, CNC); 69, *Siphona s.l.*, sp. grp. 1, sp. 28 (O27, CNC); 70, *Siphona s.l.*, sp. grp. 2, sp. 9 (O154, USNM).

← anterior

71. *Goniocera io*

72. *Goniocera versicolor*

73. *Proceromyia macronychia*

74. *Proceromyia pubioculata*

75. *Entomophaga exoleta*

76. *Entomophaga nigrohalterata*

77. *Ceromya flaviceps*

78. *Ceromya* New Guinea sp. 6

79. *Ceromya americana* complex
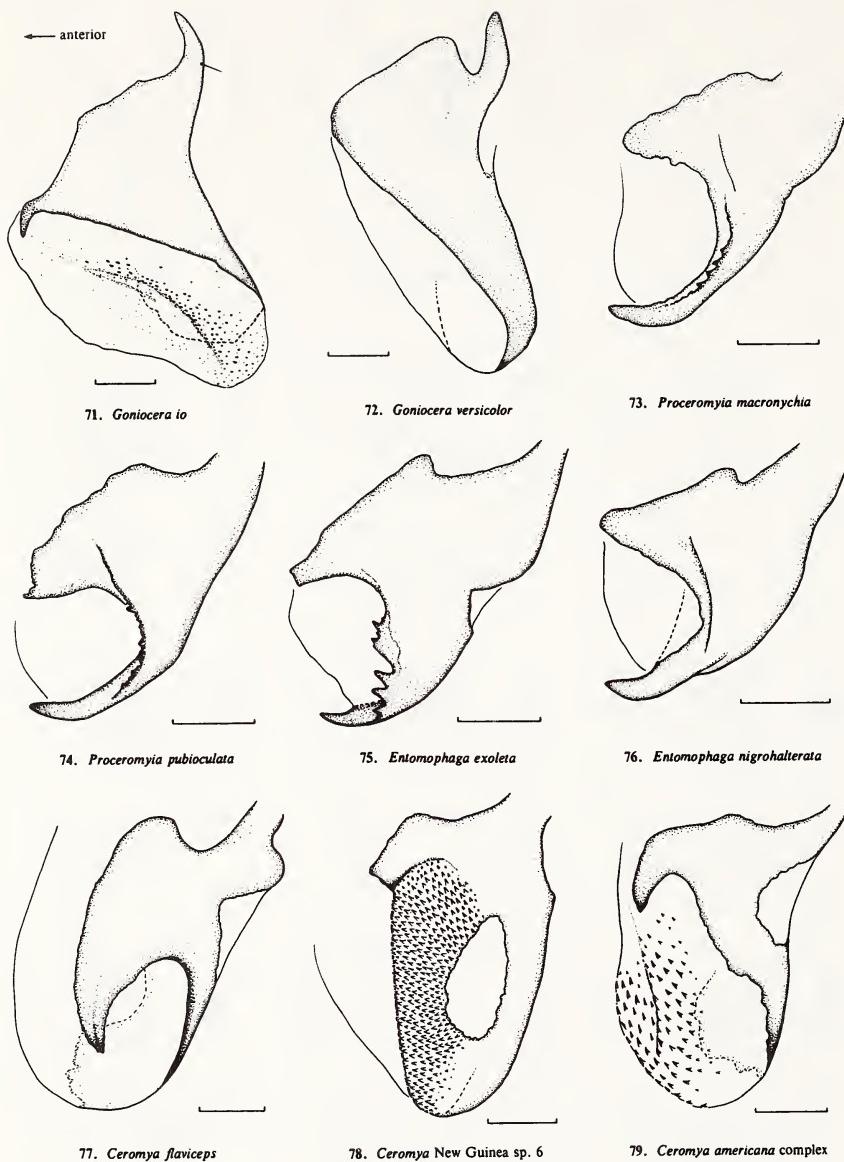
Figs. 71–79. Lateral view of left pregonite of male. Scale bars = 0.05mm: 71, *Goniocera io* (Y41, CNC); 72, *Goniocera versicolor* (Y69, CNC); 73, *Proceromyia macronychia* (Y40, CNC); 74, *Proceromyia pubioculata* (Y85, JEOH); 75, *Entomophaga exoleta* (Y132, ZMUC); 76, *Entomophaga nigrohalterata* (Y27, CNC); 77, *Ceromya flaviceps* (Y107, CNC); 78, *Ceromya* New Guinea sp. 6 (Y176, BLKU); 79, *Ceromya americana* complex (Y25, CNC).
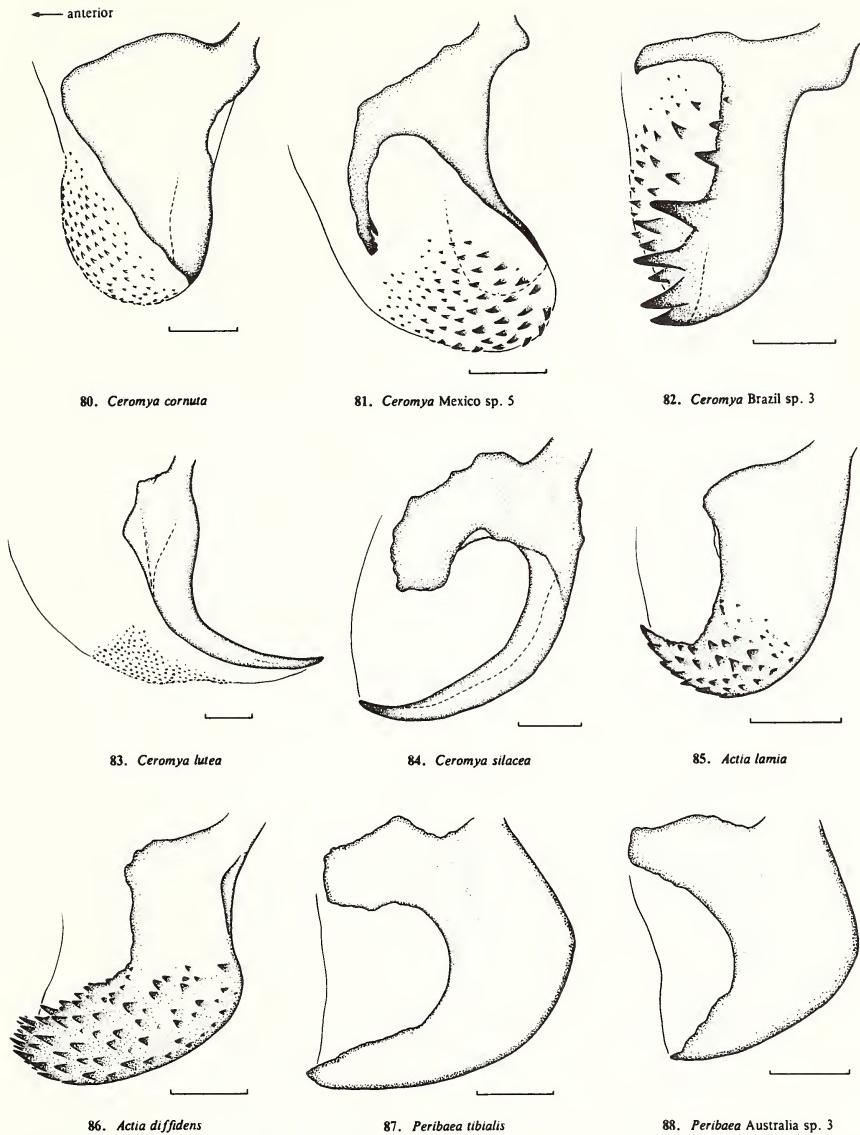
Figs. 80–88. Lateral view of left pregonite of male. Scale bars = 0.05mm: 80, *Ceromya cornuta* (Y114, CNC); 81, *Ceromya* Mexico sp. 5 (Y118, CNC); 82, *Ceromya* Brazil sp. 3 (Y125, INPA); 83, *Ceromya lutea* (Y121, CNC); 84, *Ceromya silacea* (Y179, CNC); 85, *Actia lamia* (Y17, JEOH); 86, *Actia diffidens* (Y21, CNC); 87, *Peribaea tibialis* (Y15, JEOH); 88, *Peribaea* Australia sp. 3 (Y77, DPI).

← anterior
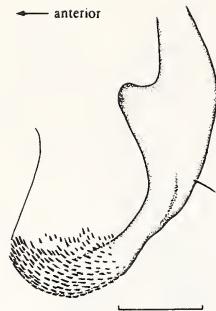
89. *S. (Actinocrocuta) singularis* complex　90. *S. (Aphantorhapha) arizonica*　91. *S. (Aphantorhaphopsis) crassulata*
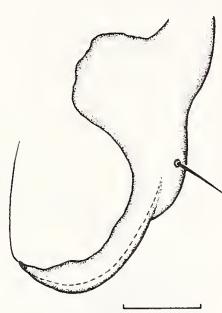
92. *S. (Aphantorhaphopsis) starkei*　93. *S. (Baeomyia) xanthogaster*　94. *S. (Ceranthia) flavipes*
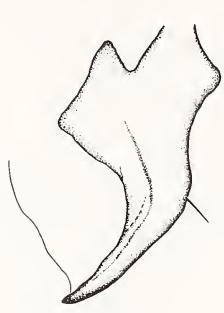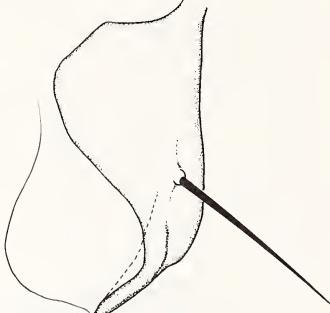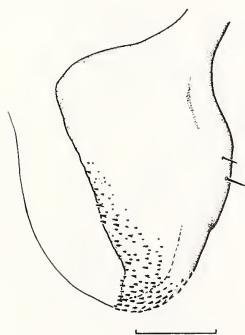
95. *S. (Pseudosiphona) brevirostris*　96. *S. (Siphona) cristata*　97. *S. (Siphonopsis) plusiae*
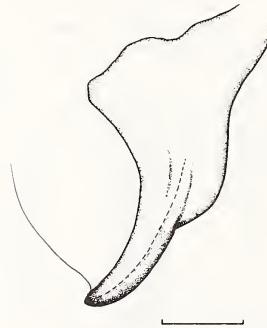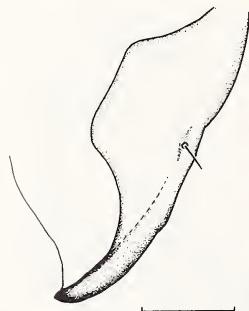
Figs. 89–97. Lateral view of left pregonite of male. Scale bars = 0.05mm: 89, *Siphona (Actinocrocuta) singularis* complex (O120, CNC); 90, *Siphona (Aphantorhapha) arizonica* (unnumbered, JEOH); 91, *Siphona (Aphantorhaphopsis) crassulata* (B3, CNC); 92, *Siphona (Aphantorhaphopsis) starkei* (B96, JEOH); 93, *Siphona (Baeomyia) xanthogaster* (B98, JEOH); 94, *Siphona (Ceranthia) flavipes* (B8, CNC); 95, *Siphona (Pseudosiphona) brevirostris* (W89, CNC); 96, *Siphona (Siphona) cristata* (W37, JEOH); 97, *Siphona (Siphonopsis) plusiae* (R97, JEOH).

98. *S. (Siphonopsis)* sp. N

99. *S. (Uruactia)* sp. 31

100. *Siphona s.l.,* sp. grp. 1, sp. 27

101. *Siphona s.l.,* sp. grp. 1, sp. 28

102. *Siphona s.l.,* sp. grp. 2, sp. 1

103. *Siphona s.l.,* sp. grp. 2, sp. 2

104. *Siphona s.l.,* sp. grp. 3, sp. 3

105. *Siphona s.l.,* sp. grp. 3, sp. 22

106. *Siphona s.l.,* unplaced sp. 1
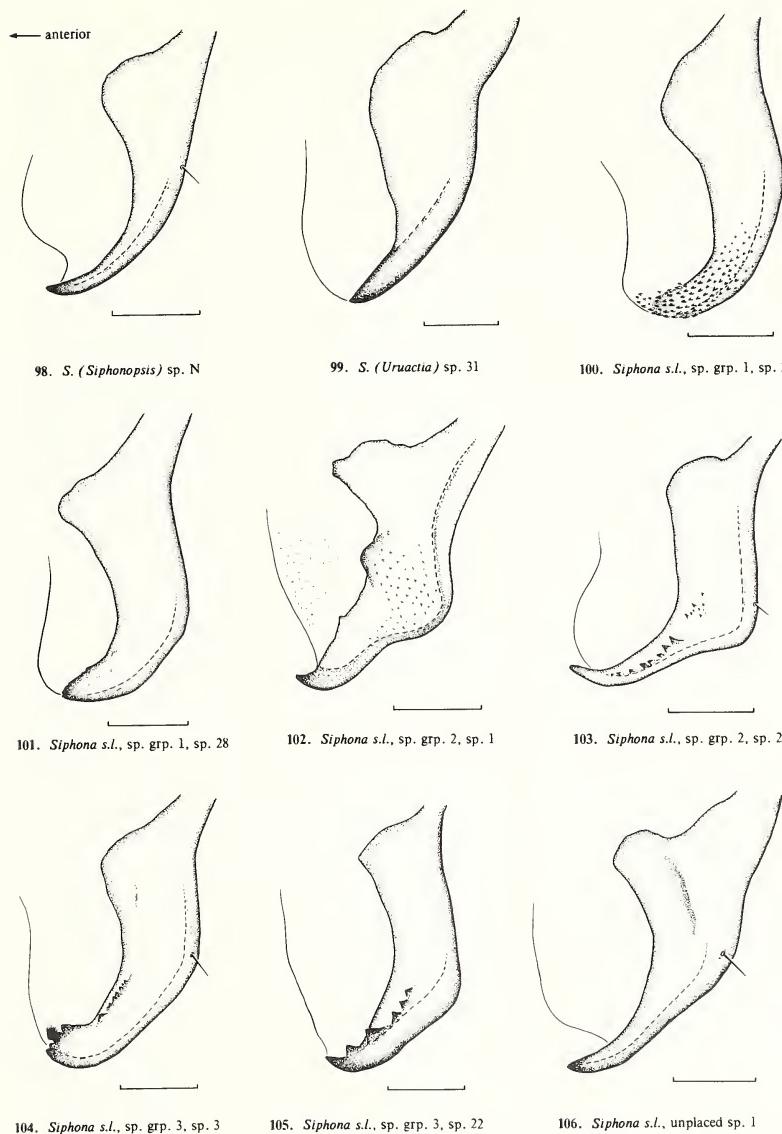
Figs. 98–106. Lateral view of left pregonite of male. Scale bars = 0.05mm: 98, *Siphona (Siphonopsis)* sp. N (O24, CNC); 99, *Siphona (Uruactia)* sp. 31 (R45, CNC); 100, *Siphona s.l.,* sp. grp. 1, sp. 27 (R46, CNC); 101, *Siphona s.l.,* sp. grp. 1, sp. 28 (O27, CNC); 102, *Siphona s.l.,* sp. grp. 2, sp. 1 (O125, JEOH); 103, *Siphona s.l.,* sp. grp. 2, sp. 2 (B92, USNM); 104, *Siphona s.l.,* sp. grp. 3, sp. 3 (B81, WSUP); 105, *Siphona s.l.,* sp. grp. 3, sp. 22 (O50, USP); 106, *Siphona s.l.,* unplaced sp. 1 (R62, WSUP).

107. *Goniocera io*   108. *Proceromyia macronychia*   109. *Proceromyia pubioculata*

110. *Entomophaga exoleta*   111. *Entomophaga nigrohalterata*   112. *Ceromya silacea*
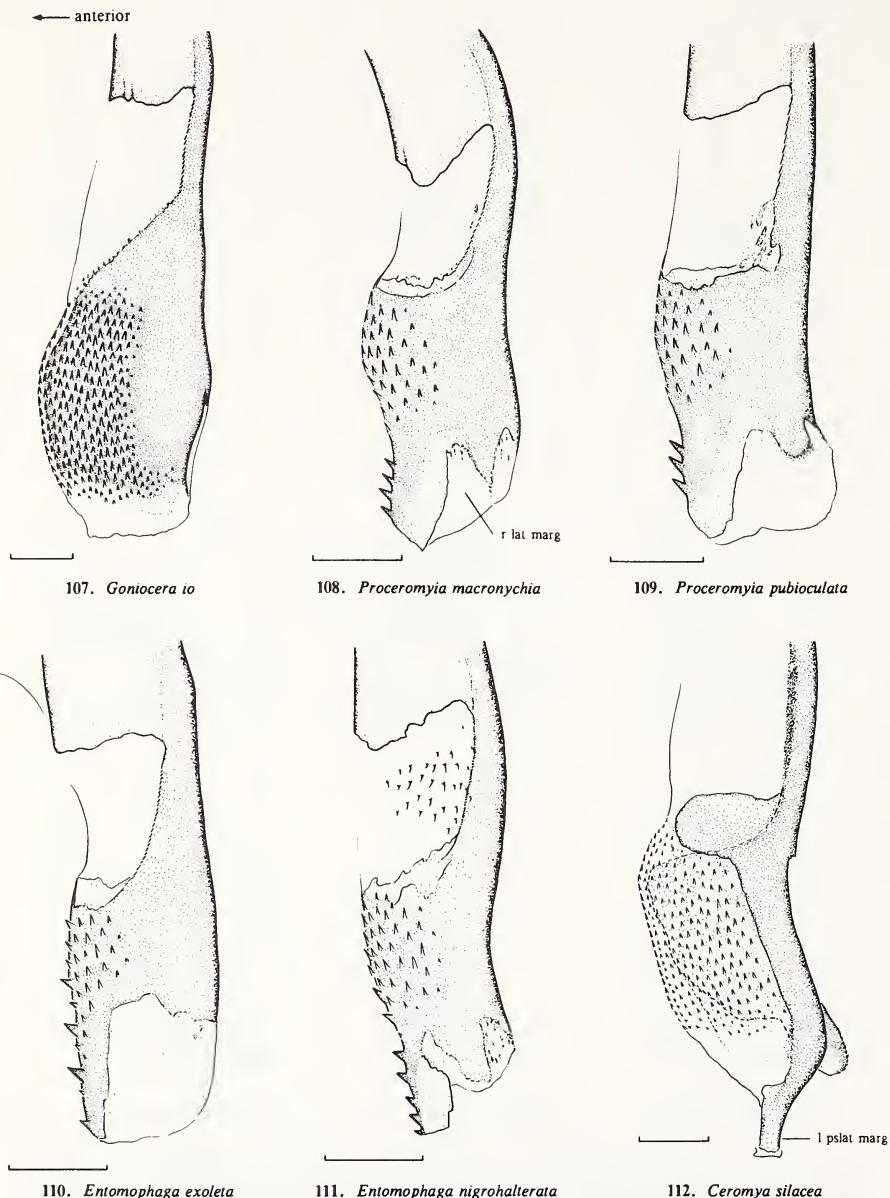
Figs. 107–112. Lateral view of male distiphallus. Scale bars = 0.05mm: 107, *Goniocera io* (Y41, CNC); 108, *Proceromyia macronychia* (Y40, CNC) (*r lat marg*, reduced lateral margin); 109, *Proceromyia pubioculata* (Y85, JEOH); 110, *Entomophaga exoleta* (Y132, ZMUC); 111, *Entomophaga nigrohalterata* (Y27, CNC); 112, *Ceromya silacea* (Y179, CNC) (*l pslat marg*, long apical extension of posterolateral margin).

113. *Ceromya flaviceps*

114. *Ceromya americana* complex

115. *Ceromya cornuta*

116. *Ceromya lutea*

117. *Actia lamia*

118. *Actia autumnalis*
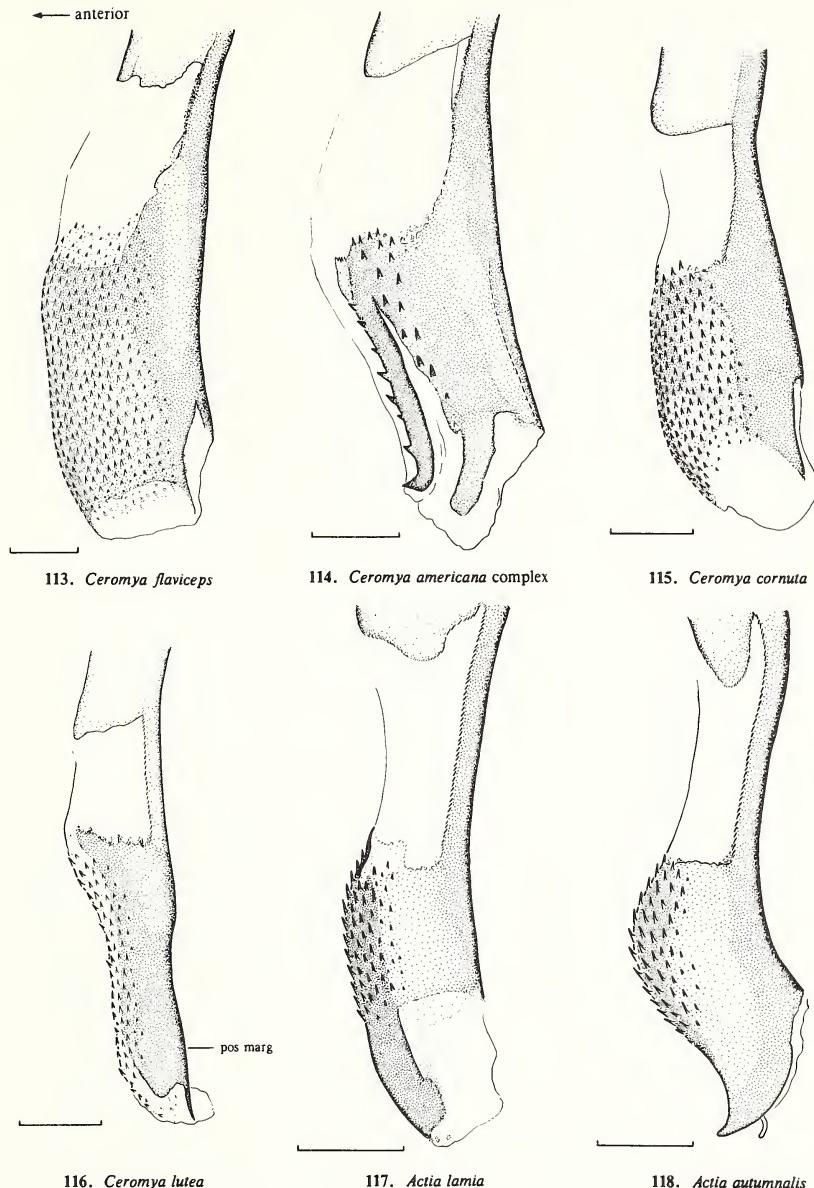
Figs. 113–118. Lateral view of male distiphallus. Scale bars = 0.05mm: 113, *Ceromya flaviceps* (Y107, CNC); 114, *Ceromya americana* complex (Y25, CNC); 115, *Ceromya cornuta* (Y114, CNC); 116, *Ceromya lutea* (Y121, CNC) (*pos marg*, posterior margin entirely sclerotized; *cf.* sclerotized projection labelled in Figs. 125, 127); 117, *Actia lamia* (Y17, JEOH); 118, *Actia autumnalis* (Y22, CNC).

← anterior
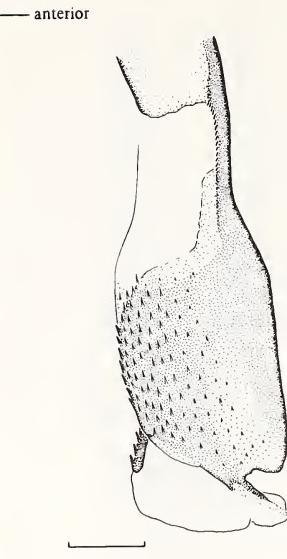
119. *Actia* New World sp. 4   **120.** *Peribaea apicalis*   **121.** *Peribaea fissicornis*
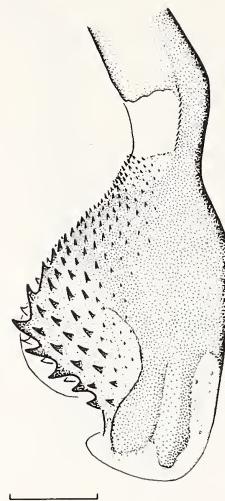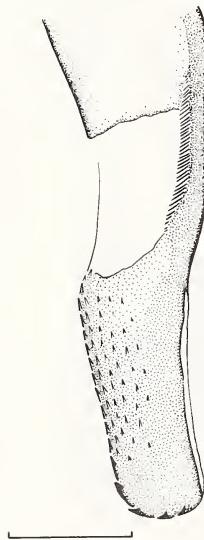
122. *S. (Actinocrocuta) singularis* complex   **123.** *S. (Actinocrocuta)* sp. 1   **124.** *S. (Aphantorhapha) arizonica*
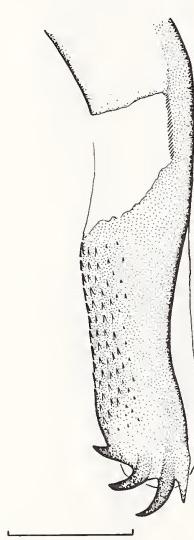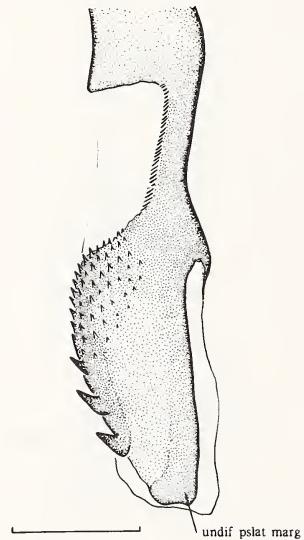
undif pslat marg

Figs. 119–124. Lateral view of male distiphallus. Scale bars = 0.05mm: 119, *Actia* New World sp. 4 (Y48, USP); 120, *Peribaea apicalis* (Y82, CNC); 121, *Peribaea fissicornis* (Y31, CNC); 122, *Siphona (Actinocrocuta) singularis* complex (O120, CNC); 123, *Siphona (Actinocrocuta)* sp. 1 (R4, CNC); 124, *Siphona (Aphantorhapha) arizonica* (unnumbered, JEOH) (*undif pslat marg*, undifferentiated posterolateral margin).

125. *S. (Aphantorhaphopsis) nigronitens*   126. *S. (Baeomyia) hurdi*   127. *S. (Ceranthia) flavipes*

128. *S. (Pseudosiphona)* sp. 1   129. *S. (Siphona) cristata*   130. *S. (Siphonopsis) plusiae*
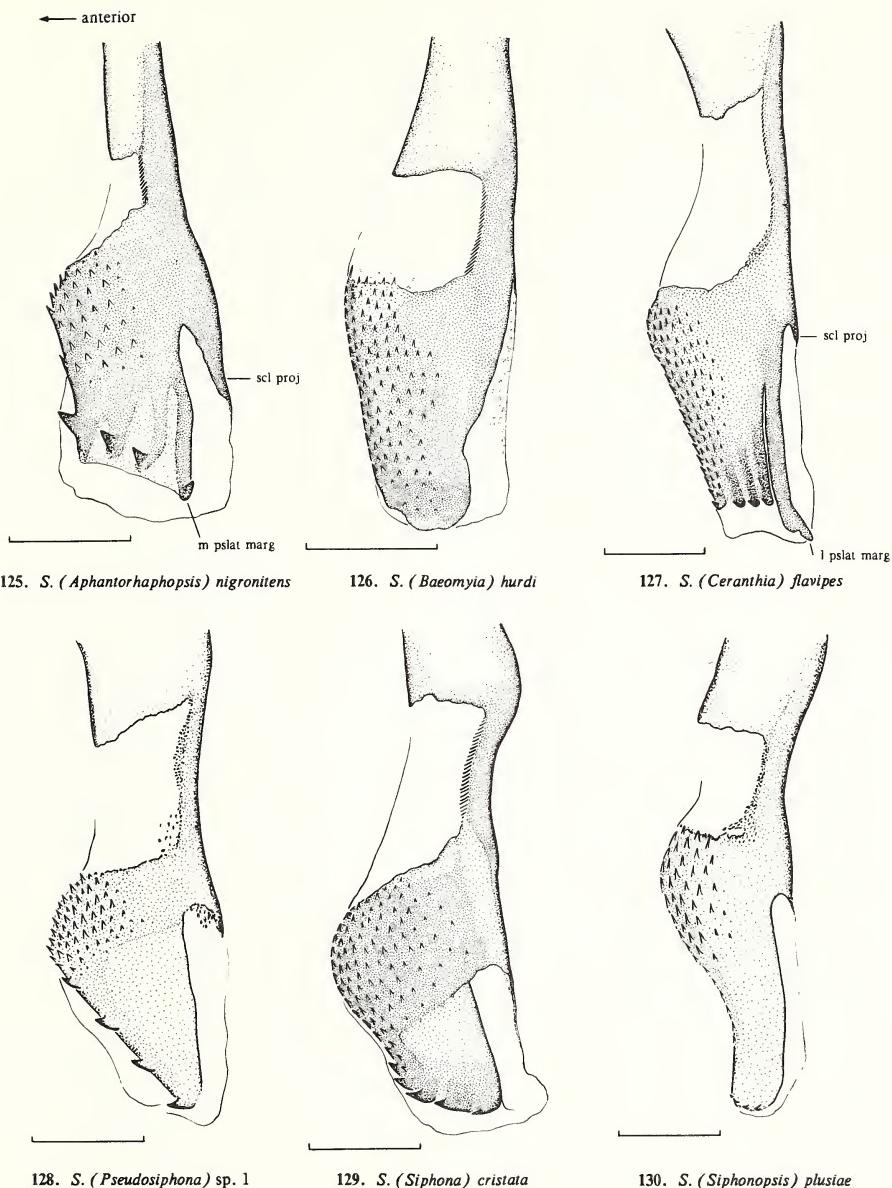
Figs. 125–130. Lateral view of male distiphallus. Scale bars = 0.05mm: 125, *Siphona (Aphantorhaphopsis) nigronitens* (R13, CNC) (*m pslat marg*, moderate apical extension of posterolateral margin beyond rest of lateral margin; *scl proj*, sclerotized projection posteriorly); 126, *Siphona (Baeomyia) hurdi* (R10, CNC); 127, *Siphona (Ceranthia) flavipes* (R81, CNC) (*l pslat marg*, long apical extension of posterolateral margin beyond rest of lateral margin; *scl proj*, sclerotized projection posteriorly); 128, *Siphona (Pseudosiphona)* sp. 1 (B69, CNC); 129, *Siphona (Siphona) cristata* (W36, JEOH); 130, *Siphona (Siphonopsis) plusiae* (B18, CNC).

← anterior

131. *S. (Uruactia)* sp. 31

132. *Siphona s.l.*, sp. grp. 1, sp. 25

133. *Siphona s.l.*, sp. grp. 2, sp. 1

134. *Siphona s.l.*, sp. grp. 2, sp. 3

135. *Siphona s.l.*, sp. grp. 3, sp. 3

136. *Siphona s.l.*, unplaced sp. 1
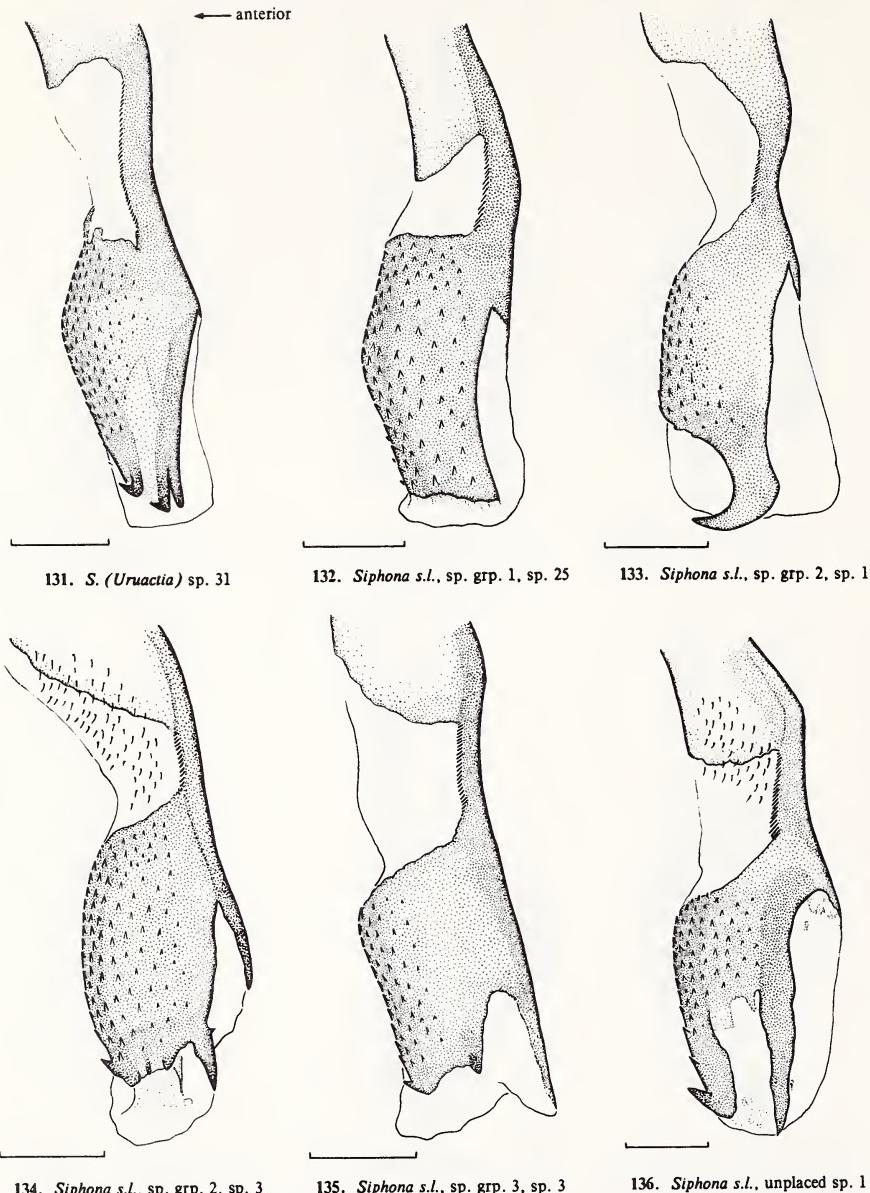
Figs. 131–136. Lateral view of male distiphallus. Scale bars = 0.05mm: 131, *Siphona (Uruactia)* sp. 31 (R45, CNC); 132, *Siphona s.l.*, sp. grp. 1, sp. 25 (R2, CNC); 133, *Siphona s.l.*, sp. grp. 2, sp. 1 (O148, CAS); 134, *Siphona s.l.*, sp. grp. 2, sp. 3 (R65, CNC); 135, *Siphona s.l.*, sp. grp. 3, sp. 3 (B81, WSUP); 136, *Siphona s.l.*, unplaced sp. 1 (R62, WSUP).
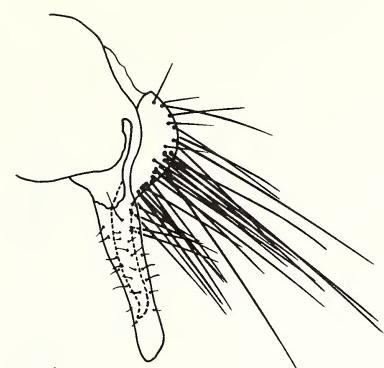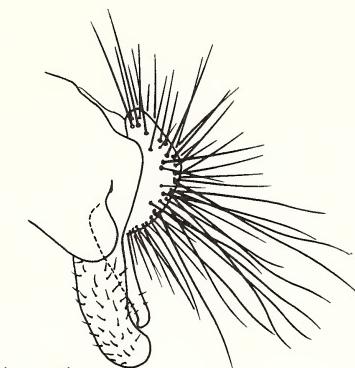
137. *Goniocera io*   138. *Ceromya americana* complex
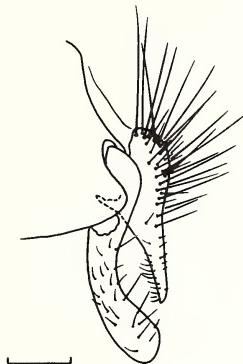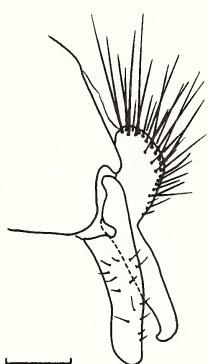
139. *Peribaea apicalis*   140. *S. (Pseudosiphona)* sp. 1   141. *S. (Siphona) cristata*
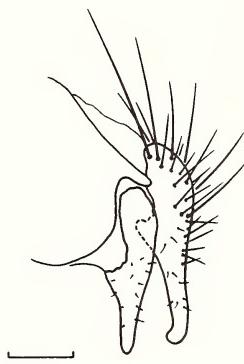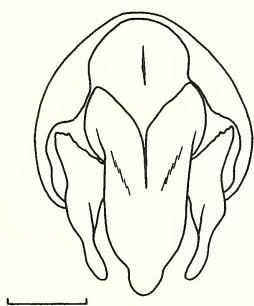
142. *S. (Actinocrocuta)*   143. *S. (Aphantorhapha)* sp. 1   144. *S. (Siphona) kairiensis*
    singularis complex
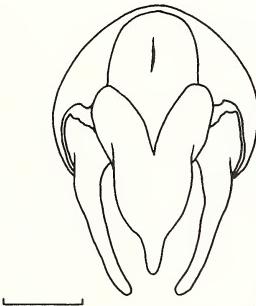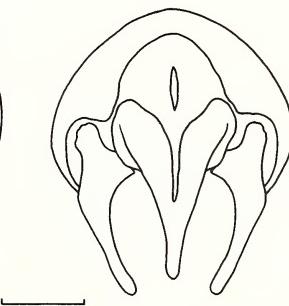
Figs. 137–141. Lateral view of male surstylus and cerci. Scale bars = 0.1mm: 137, *Goniocera io* (Y41, CNC); 138, *Ceromya americana* complex (Y25, CNC); 139, *Peribaea apicalis* (Y82, CNC); 140, *Siphona (Pseudosiphona)* sp. 1 (B69, CNC); 141, *Siphona (Siphona) cristata* (W36, JEOH). Figs. 142–144. Posterior view of male genitalia, vestiture omitted. Scale bars = 0.1mm: 142, *Siphona (Actinocrocuta) singularis* complex (lectotype of *S. chaetosa* (Tnsd.), USNM); 143, *Siphona (Aphantorhapha)* sp. 1 (O182, BMNH); 144, *Siphona (Siphona) kairiensis* (holotype, CAS).
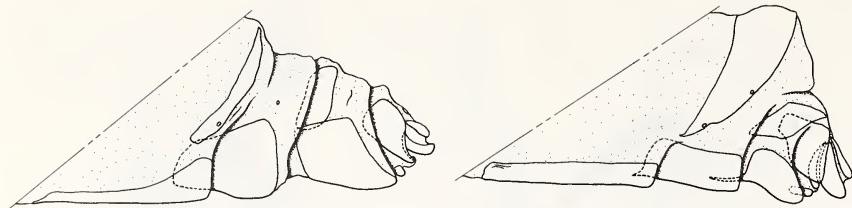
145. *Goniocera io*

146. *Proceromyia macronychia*
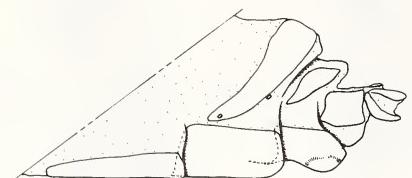
ant apod

147. *Entomophaga nigrohalterata*
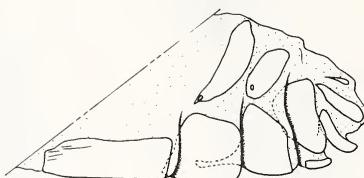
148. *Ceromya silacea*

Figs. 145–148. Lateral and ventral views of female genitalia. Scale bars = 0.2mm: 145, *Goniocera io* (Y63, CNC); 146, *Proceromyia macronychia* (Y134, CNC); 147, *Entomophaga nigrohalterata* (Y135, CNC) (*ant apod*, anterior apodeme of sternum 7); 148, *Ceromya silacea* (Y137, CNC).
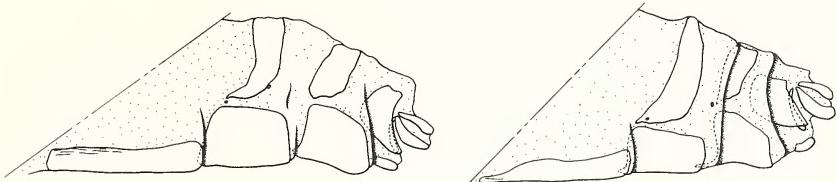
149. *Ceromya flaviceps*
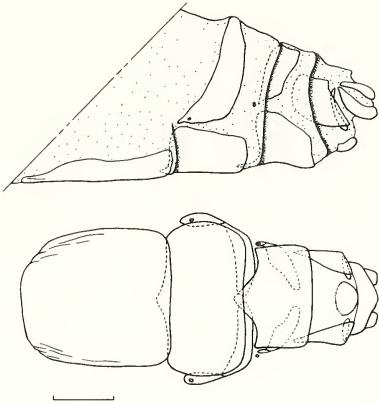
150. *Ceromya ontario*
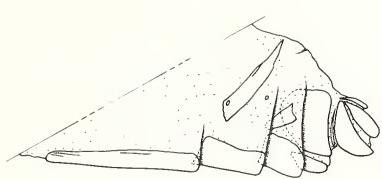
151. *Actia interrupta*
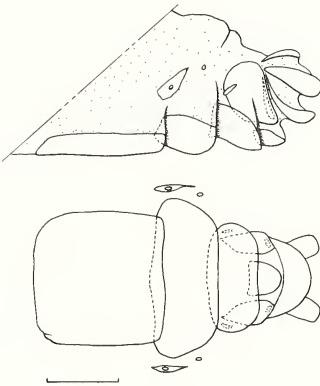
152. *Actia* Zaire sp. 1

Figs. 149–152. Lateral and ventral views of female genitalia. Scale bars = 0.2mm: 149, *Ceromya flaviceps* (Y133, CNC); 150, *Ceromya ontario* (Y65, USNM); 151, *Actia interrupta* (Y74, JEOH); 152, *Actia* Zaire sp. 1 (Y105, CNC).
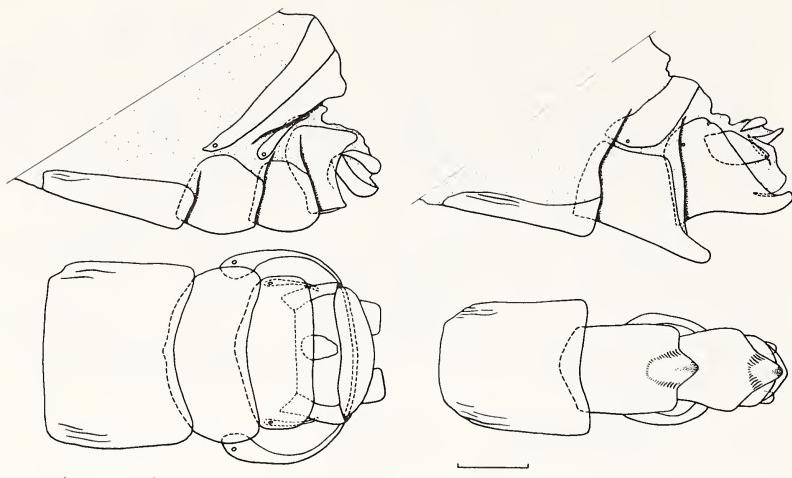
153. *Peribaea fissicornis*

154. *Peribaea* Africa sp. 5
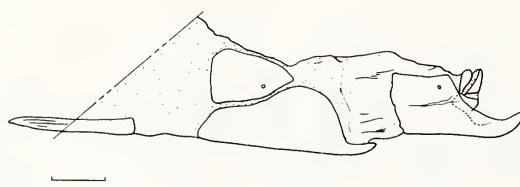
155. *Peribaea ugandana*
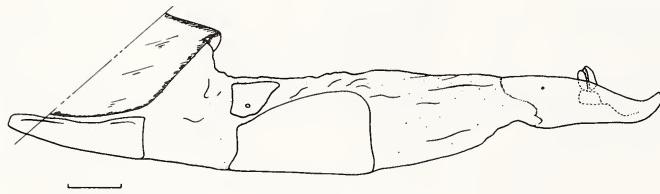
156. *Peribaea* Australia sp. 1

Figs. 153–156. Lateral and ventral views of female genitalia. Scale bars = 0.2mm: 153, *Peribaea fissicornis* (Y60, JEOH); 154, *Peribaea* Africa sp. 5 (Y96, USNM); 155, *Peribaea ugandana* (Y93, USNM); 156, *Peribaea* Australia sp. 1 (Y84, DPI).
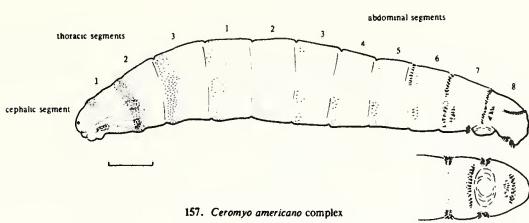
157. *Ceromyo americano* complex

158. *Goniocero io*

159. *Ceromyo siloceo*
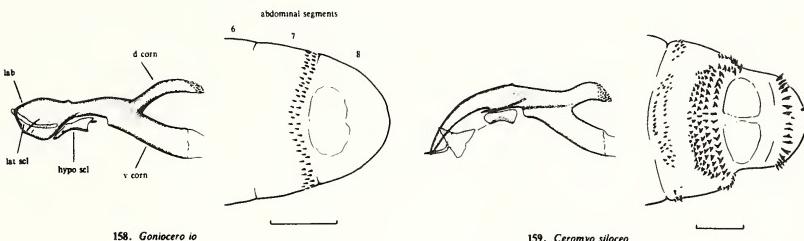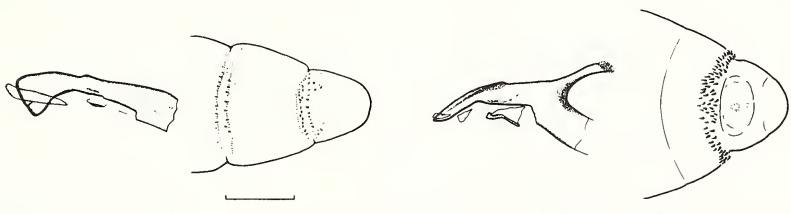
160. *Actia lamia*

161. *Peribaeo ugondono*
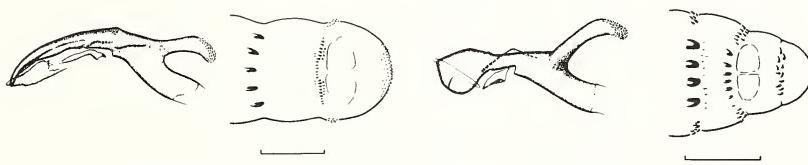
162. *S. (Pseudosiphona)* sp. 14

163. *S. (Siphona)* lutea

Fig. 157. Lateral view of first instar of *Ceromya americana* complex, with ventral view of abdominal segments 6 to 8 (Y73, UCB). Scale bar = 0.1mm. Figs. 158–163. Lateral view of cephalopharyngeal skeleton and ventral view of abdominal segments 6 to 8 of first instars. Scale bars = 0.05mm: 158, *Goniocera io* (CNC slide) (*d corn*, dorsal cornu; *hypo scl*, hypopharyngeal sclerite; *lat scl*, lateral sclerite; *lab*, labrum; *v corn*, ventral cornu); 159, *Ceromya silacea* (Y137, CNC); 160, *Actia lamia* (Y75, CNC); 161, *Peribaea ugandana* (Y93, USNM); 162, *Siphona (Pseudosiphona)* sp. 14 (B93, CNC); 163, *Siphona (Siphona) lutea* (W44, CNC).

HOSTS

Introduction

Hosts are recorded for over 60 siphonine species, or about 20% of the described fauna, in Table 2. It is difficult to speculate about host preferences from such meagre information, though a few general patterns are suggested by this compilation of host records. Most apparent is that siphonines are primarily parasitoids of larval Lepidoptera, as host species are known from only three families in other orders, the Pyrrhocoridae (Hemiptera), Tenthredinidae (Hymenoptera) and Tipulidae (Diptera).

Within the Lepidoptera there is marked preference for the Macrolepidoptera, with only *Peribaea* and *Actia* known with certainty from hosts in both the Microlepidoptera and Macrolepidoptera. Within the Macrolepidoptera the Geometridae are parasitized by species in the most supraspecific taxa (nine), followed closely by the Noctuidae (seven). *Actia* seems the most generalized siphonine group in terms of host preference, with records from nine families of Microlepidoptera and six families of Macrolepidoptera, though this may in part be attributable to the large number of hosts known for this genus.

A brief section about hosts follows each generic or subgeneric description in the Classification chapter of this work. Because no striking patterns of host preference are evident between siphonine groups, and hosts are still inadequately known, host information is not used in the phylogenetic analysis of the Siphonini.

Explanation of parasite-host list

Table 2 is a compilation of the known hosts of siphonine species. Almost all records have been taken from the literature, though a few are new. New records were obtained from label data and are accompanied in Table 2 by the museum where specimens bearing the listed host data are deposited.

Siphonine species names are listed in bold face and their hosts in italics. The former are listed alphabetically by genus and species and the latter first by family and second by genus and species (thereby grouping together host species belonging to the same family). Siphonine names are those used herein, and an attempt has been made to update host names to correspond with current usage.

The literature includes many host records for tachinids that are unreliable because of questionable species identifications. The records used here are mostly from critically compiled works published by tachinid specialists, and as such are more reliable than the primary literature (though even these authors undoubtedly repeat some published errors because of the paucity of information about most siphonine species).

Where records or species identifications were listed as questionable in a reference cited here, I have preceded the questionable name with a question mark.

Table 2. Parasite-host list for world Siphonini

SIPHONINE & HOST SPECIES	FAMILY	REFERENCE
***Actia crassicornis* (Meigen)**		
Depressaria applana Fabr.	Oecophoridae	Lundbeck, 1927:461; Herting, 1960:60; Mesnil, 1963a:817
Depressaria astrantiae Heinem.	Oecophoridae	Herting, 1960:60; Mesnil, 1963a:817
Depressaria bupleurella Heinem.	Oecophoridae	Herting, 1960:60; Mesnil, 1963a:817
Depressaria costosa Haworth	Oecophoridae	Herting, 1960:60; Mesnil, 1963a:817
Depressaria depressella Hb.	Oecophoridae	Herting, 1960:60; Mesnil, 1963a:817
Depressaria heydenii Zeller	Oecophoridae	Lundbeck, 1927:461; Herting, 1960:60; Mesnil, 1963a:817
Depressaria hippomarathri Nick.	Oecophoridae	Herting, 1960:60; Mesnil, 1963a:817
Depressaria liturella Schiff.	Oecophoridae	Herting, 1960:60; Mesnil, 1963a:817
Sparganothis pilleriana Sch.	Tortricidae	Herting, 1960:60; Mesnil, 1963a:817
Tortrix viridana L.	Tortricidae	Lundbeck, 1927:461; Herting, 1960:60; Mesnil, 1963a:817
Yponomeuta mallinellus Z.	Yponomeutidae	Hubenov, 1985:29
***Actia diffidens* Curran**		
Acleris variana Fernald	Tortricidae	Prebble, 1935; Arnaud, 1978:52
Choristoneura conflictana Walker	Tortricidae	Arnaud, 1978:52
Spilonota ocellana Denis & Schiff.	Tortricidae	Arnaud, 1978:52
***Actia eucosmae* Bezzi**		
Crocidosema plebeiana Zeller	Tortricidae	Crosskey, 1973:176; Chadwick & Nikitin, 1985:588
***Actia hargreavesi* Curran**		
Dysdercus sp. (Hemiptera)	Pyrrhocoridae	Mesnil, 1963a:814 (as *Actia comitata*) (doubtful record)
***Actia infantula* (Zett.)**		
Monopis rusticella Hübner	Tineidae	Herting, 1960:61; Mesnil, 1963a:819
***Actia interrupta* Curran**		
Melanolophia imitata Walker	Geometridae	Arnaud, 1978:53
Schizura concinna Smith	Notodontidae	Arnaud, 1978:53
Acleris variana Fernald	Tortricidae	Arnaud, 1978:53
Acleris variegana Denis & Schiff.	Tortricidae	Arnaud, 1978:53
Amorbia cuneana Walsingham	Tortricidae	Arnaud, 1978:53; Oatman *et al.*, 1983:53
Archippus packardianus Fernald	Tortricidae	Arnaud, 1978:53
Archips argyrospilus Walker	Tortricidae	Arnaud, 1978:53
Archips rosanus L.	Tortricidae	Arnaud, 1978:54
Choristoneura conflictana Walker	Tortricidae	Arnaud, 1978:54
Choristoneura fumiferana Clemens	Tortricidae	Arnaud, 1978:54
Choristoneura pinus Freeman	Tortricidae	Arnaud, 1978:54
Choristoneura rosaceana Harris	Tortricidae	Arnaud, 1978:54
Croesia albicomana Clemens	Tortricidae	Arnaud, 1978:54
Epinotia crenana Hübner	Tortricidae	Arnaud, 1978:53
Epinotia emarginana Walsingham	Tortricidae	Arnaud, 1978:53

Table 2 (continued)

SIPHONINE & HOST SPECIES	FAMILY	REFERENCE
Grapholitha molesta Busck	Tortricidae	Arnaud, 1978:53
Phalonia oenotherana Riley	Tortricidae	Arnaud, 1978:54
Xenotemna pallorana Robinson	Tortricidae	Arnaud, 1978:54
Actia near *interrupta* Curran		
Archips cerasivoranus Fitch	Tortricidae	Arnaud, 1978:55
Archips fervidanus Clemens	Tortricidae	Arnaud, 1978:55
***Actia jocularis* Mesnil**		
Lymantria dispar L.	Lymantriidae	Schaefer & Shima, 1981:370
***Actia lamia* (Meigen)**		
Ourapteryx sambucaria L.	Geometridae	Herting, 1960:60; Mesnil, 1963a:822
Lasiocampa querus L.	Lasiocampidae	Wainwright, 1928:208; Herting, 1960:60; Mesnil, 1963a:822
Epiblema luctuosana Dup.	Tortricidae	Herting, 1960:60; Mesnil, 1963a:822
Epiblema pflugiana Haworth	Tortricidae	Lundbeck, 1927:460; Herting, 1960:60; Mesnil, 1963a:822
Laspeyresia cosmophorana Treitschke	Tortricidae	Mesnil, 1963a:822
***Actia maksymovi* Mesnil**		
Cacoecia murinana Hübner	Tortricidae	Herting, 1960:61; Mesnil, 1963a:823
Semasia diniana Hübner	Tortricidae	Herting, 1960:61; Mesnil, 1963a:823
Spilonota lariciana Hein.	Tortricidae	Herting, 1960:61; Mesnil, 1963a:823
Actia near *maksymovi* Mesnil		
Dioryctria abietella Denis & Schiff.	Pyralidae	Crosskey, 1976a:291
***Actia nigroscutellata* Lundbeck**		
Elachista megerleella Staint.	Elachistidae	Herting, 1960:61; Mesnil, 1963a:825
Laspeyresia cosmophorana Tr.	Tortricidae	Mesnil, 1963a:825
Laspeyresia servillana Dup.	Tortricidae	Herting, 1960:61 (as questionable); Mesnil, 1963a:825
Olethreutes roseomaculana Herr.-Sch. or *Olethreutes dalecarliana* Guenée	Tortricidae	Lundbeck, 1927:463; Herting, 1960:61; Mesnil, 1963a:825
Semasia ustomaculana Curtis	Tortricidae	Lundbeck, 1927:463; Herting, 1960:61; Mesnil, 1963a:825
Tortrix viridana L.	Tortricidae	Hubenov, 1985:29
***Actia nudibasis* Stein**		
Heringia dodecella L.	Gelechiidae	Herting, 1960:60; Mesnil, 1963a:826
Dioryctria splendidella Herr.-Sch.	Pyralidae	Herting, 1960:60; Mesnil, 1963a:826; Shima, 1970c:187
Evetria buoliana Schiff.	Tortricidae	Lundbeck, 1927:459; Herting, 1960:61; Mesnil, 1963a:826

Table 2 (continued)

SIPHONINE & HOST SPECIES	FAMILY	REFERENCE
Evetria resinella L.	Tortricidae	Lundbeck, 1927:459; Herting, 1960:60; Mesnil, 1963a:826
Actia painei Crosskey		
Agonoxena pyrogramma Meyrick	Agonoxenidae	Crosskey, 1962:175
Actia pamirica Richter		
Parapandemis chondrillana H. S.	—	Richter, 1974:1269
Spilonota ocellana F.	Tortricidae	Richter, 1974:1269
Actia parviseta Malloch		
Isotenes miserana Walker	Tortricidae	Crosskey, 1973:176; Chadwick & Nikitin, 1985:590
Actia pilipennis (Fallén)		
Platyptilia rhododactyla Schiff.	Pterophoridae	Herting, 1960:59
Acalla aspersana Hübner	Tortricidae	Herting, 1960:59; Mesnil, 1963a:828
Acalla hastiana L.	Tortricidae	Mesnil, 1963a:828
Acalla logiana Schiff.	Tortricidae	Herting, 1960:59; Mesnil, 1963a:828
Ancylis mitterbacheriana Schiff.	Tortricidae	Herting, 1960:59; Mesnil, 1963a:828
Ancylis tineana Hübner	Tortricidae	Herting, 1960:59; Mesnil, 1963a:828
Capua angustiorana Haworth	Tortricidae	Herting, 1960:59; Mesnil, 1963a:828
Eucosma sordidana Hübner	Tortricidae	Mesnil, 1963a:828
Olethreutes schulziana Fabr.	Tortricidae	Mesnil, 1963a:828
Sparganothis pilleriana Schiff.	Tortricidae	Herting, 1960:59; Mesnil, 1963a:828
Tortrix bergmanniana L.	Tortricidae	Herting, 1960:59; Mesnil, 1963a:828
Tortrix loefflingiana L.	Tortricidae	Herting, 1960:59; Mesnil, 1963a:828; Hubenov, 1985:29
Tortrix pronubana Hübner	Tortricidae	Herting, 1960:59; Mesnil, 1963a:828
Tortrix viridana L.	Tortricidae	Herting, 1960:59; Mesnil, 1963a:828; Hubenov, 1985:29
Actia spp. (North America)		
Phyganidia californica Packard	Dioptidae	Arnaud, 1978:56
Gnorimoschema spp.	Gelechiidae	Arnaud, 1978:56
Catocala relicta Walker	Noctuidae	Arnaud, 1978:56
Heterocampa guttivitta Walker	Notodontidae	Arnaud, 1978:56
Epinotia similana Hübner	Tortricidae	Arnaud, 1978:56
Episimus argutanus Clemens	Tortricidae	Arnaud, 1978:56
Actia spp. (Old World)		
Gaesa bisignella Snellen	Gelechiidae	Crosskey, 1976a:291
Herpetogramma licarsisalis Walker	Pyralidae	Cantrell, 1986:259
Epiphyas postvittana Walker	Tortricidae	Cantrell, 1986:259
Ceromya americana (Townsend)		
Schizura concinna Smith	Notodontidae	Arnaud, 1978:51

Table 2 (continued)

SIPHONINE & HOST SPECIES	FAMILY	REFERENCE
***Ceromya apicipunctata* (Malloch)**		
Unidentified sp.	Noctuidae	Crosskey, 1976a:291
***Ceromya bicolor* (Meigen)**		
Phragmatobia fuliginosa L.	Arctiidae	Herting, 1960:61; Mesnil, 1963a:835
Dendrolimus pini L.	Lasiocampidae	Herting, 1960:61; Mesnil, 1963a:835
Eriogaster lanestris L.	Lasiocampidae	Lundbeck, 1927:466; Herting, 1960:61; Mesnil, 1963a:835
Gastropacha quercifolia L.	Lasiocampidae	Herting, 1960:61; Mesnil, 1963a:835
Lasiocampa quercus L.	Lasiocampidae	Lundbeck, 1927:466; Herting, 1960:61; Mesnil, 1963a:835
Dolerus pratensis L. (Hymenoptera)	Tenthredinidae	Mesnil, 1963a:835
***Ceromya cibdela* (Villeneuve)**		
Stylochilus sp.	Sphingidae	New record (CNC)
***Ceromya ?fergusoni* (Bezzi)**		
Unidentified sp.	Geometridae	Crosskey, 1973:176
***Ceromya luteicornis* (Curran)**		
Unidentified sp.	Saturniidae	Curran, 1933c:162
Nudaurelia belina	—	Curran, 1933c:162
***Ceromya ontario* (Curran)**		
Ennomos subsignarius Hübner	Geometridae	Arnaud, 1978:55
***Ceromya palloris* (Coquillett)**		
Drepana arcuata Walker	Drepanidae	Arnaud, 1978:55
Drepana bilineata Packard	Drepanidae	Arnaud, 1978:55
***Ceromya* near *palloris* (Coquillett)**		
Ennomos subsignarius Hübner	Geometridae	Arnaud, 1978:55
Eugonobapta nivosaria Guenée	Geometridae	Arnaud, 1978:55
***Ceromya patellicornis* Mesnil**		
Callopistria repleta Walker	Noctuidae	Crosskey, 1976a:291
***Ceromya pruinosa* Shima**		
Dendrolimus undans flaveola Motsch.	Lasiocampidae	Shima, 1973:155
***Ceromya silacea* (Meigen)**		
Erastria fasciana L.	Noctuidae	Herting, 1960:61; Mesnil, 1963a:839
***Ceromya* spp. (Australia)**		
Ectropis excursaria Guenée	Geometridae	Cantrell, 1986:259
Chrysodeixis argentifera Guenée	Noctuidae	Cantrell, 1986:259
Euplexia nigerrima Guenée	Noctuidae	Cantrell, 1986:259

Table 2 (continued)

SIPHONINE & HOST SPECIES	FAMILY	REFERENCE
Homoeosoma vagella Zeller	Pyralidae	Cantrell, 1986:259
Goniocera io (Aldrich)		
Malacosoma americanum Fab.	Lasiocampidae	Arnaud, 1978:126
Malacosoma disstria Hübner	Lasiocampidae	Arnaud, 1978:126
Goniocera schistacea (B.B.)		
Malacosoma castrensis L.	Lasiocampidae	Herting, 1960:119; Mesnil, 1963:801
Goniocera versicolor (Fallén)		
Malacosoma neustria L.	Lasiocampidae	Herting, 1960:120; Mesnil, 1963:803
Peribaea argentifrons (Malloch)		
Copromorpha prasinochroa Meyrick	Copromorphidae	Crosskey, 1973:176; Chadwick & Nikitin, 1985:592
Homoeosoma vagella Zeller	Pyralidae	Crosskey, 1973:176
Peribaea fissicornis (Strobl)		
Angerona prunaria L.	Geometridae	Herting, 1960:59; Mesnil, 1963a:807
Boarmia bistortata Goeze	Geometridae	Herting, 1960:59; Mesnil, 1963a:807
Boarmia consortaria Fabr.	Geometridae	Herting, 1960:59; Mesnil, 1963a:807
Bupalus piniarius L.	Geometridae	Herting, 1960:59; Mesnil, 1963a:807
Himera pennaria L.	Geometridae	Herting, 1960:59; Mesnil, 1963a:807
Ourapteryx sambucaria L.	Geometridae	Herting, 1960:59; Mesnil, 1963a:807
Phigalia pedaria Fabr.	Geometridae	Herting, 1960:59; Mesnil, 1963a:807
Poecilocampa populi L.	Lasiocampidae	Herting, 1960:59; Mesnil, 1963a:807
Peribaea hyalinata (Malloch)		
Hyblaea puera Cramer	Hyblaeidae	Crosskey, 1976a:291
Pyrausta machoeralis Walker	Pyralidae	Crosskey, 1976a:291
Peribaea orbata (Wiedemann)		
Acantholeucania loreyi Dup.	Noctuidae	Crosskey, 1973:176
Aedia leucomelas	Noctuidae	Shima, 1981:450
"Cirphis" sp.	Noctuidae	Crosskey, 1976a:291
Earias sp(p).	Noctuidae	Mesnil, 1963a:806
Heliothis armigera Hübner	Noctuidae	Shima, 1981:450; Crosskey, 1976a:291
Heliothis sp.	Noctuidae	Crosskey, 1973:176
Laphygma sp(p).	Noctuidae	Mesnil, 1963a:806
Leucania separata	Noctuidae	Shima, 1981:450
Leucania venalba Moore	Noctuidae	Shima, 1981:450; Crosskey, 1976a:291
Mythimna convecta Walker	Noctuidae	Broadley, 1986:61
Platysenta dolorosa Walker	Noctuidae	Cantrell, 1986:259
Prodenia sp(p).	Noctuidae	Mesnil, 1963a:806
Pseudaletia unipuncta Haworth	Noctuidae	Shima, 1981:450; Crosskey, 1973:176 & 1976a:291
Spodoptera exempta Walker	Noctuidae	Crosskey, 1973:176
Spodoptera exigua Hübner	Noctuidae	Shima, 1981:450; Crosskey, 1976a:291
Spodoptera littoralis Boisd.	Noctuidae	Kugler, 1979:56

Table 2 (continued)

SIPHONINE & HOST SPECIES	FAMILY	REFERENCE
Spodoptera litura Fabr.	Noctuidae	Shima, 1981:450; Crosskey, 1973:176 & 1976a:291; Jayanth & Nagarkatti, 1984:77
Spodoptera mauritia Boisd.	Noctuidae	Shima, 1981:450; Crosskey, 1976a:291
Spodoptera sp(p).	Noctuidae	Mesnil, 1963a:806
Hedylepta indicata	Pyralidae	Shima, 1981:450
Peribaea palaestina (Villeneuve)		
Spodoptera exigua Hübner	Noctuidae	Kugler, 1979:56
Spodoptera littoralis Boisd.	Noctuidae	Kugler, 1979:56
Peribaea plebeia (Malloch)		
Earias huegeli Rogenhofer	Noctuidae	Crosskey, 1973:176
Peribaea sp. ? plebeia (Malloch)		
? Anthela sp.	Anthelidae	Crosskey, 1973:176; Chadwick & Nikitin, 1985:592
Peribaea stiglinae (Bezzi)		
Stiglina superior Butl.	Thyrididae	Bezzi, 1928:204
Peribaea suspecta (Malloch)		
Earias vittella Fabr.	Noctuidae	Crosskey, 1976a:291
Earias sp.	Noctuidae	Curran, 1928:237; Crosskey, 1976a:291
Peribaea tibialis (Robineau-Desvoidy)		
Ennomos autumnaria Wornb.	Geometridae	Hubenov, 1985:29
Ennomos quercinaria Hufn.	Geometridae	Hubenov, 1985:29
Prosopolopha jourdanaria Vill.	Geometridae	Herting, 1960:59; Mesnil, 1963a:813
Lasiocampa grandis Stgr.	Lasiocampidae	Herting, 1960:59; Mesnil, 1963a:813; Kugler, 1979:56
Orgyia dubia Tausch.	Lymantriidae	Herting, 1960:59; Mesnil, 1963a:813; Kugler, 1979:55
Anarta myrtilli L.	Noctuidae	Herting, 1960:59; Mesnil, 1963a:813
Asticta pastinum Tr.	Noctuidae	Mesnil, 1963a:813
Spodoptera exigua Hübner	Noctuidae	Kugler, 1979:56
Yponomeuta malinellus Z.	Yponomeutidae	Hubenov, 1985:29
Peribaea sp. (Australia)		
Spodoptera exigua Hübner	Noctuidae	Cantrell, 1986:259
Crocidosema plebejana Zeller	Tortricidae	Cantrell, 1986:259
S. (Aphantorhaphopsis) mallochiana (Gardner)		
Pelopidas mathias Fabr.	Hesperiidae	Crosskey, 1976a:291
"Turmeric skipper"	Hesperiidae	Crosskey, 1976a:291
"Ginger lily leaf-roller"	Hesperiidae	Crosskey, 1976a:291

Table 2 (continued)

SIPHONINE & HOST SPECIES	FAMILY	REFERENCE
"Rice leaf-roller skipper"	Hesperiidae	Crosskey, 1976a:291
S. (*Aphantorhaphopsis*) *norma* (Malloch)		
Mythimna convecta Walker	Noctuidae	Crosskey, 1973:176; Chadwick & Nikitin, 1985:590
S. (*Aphantorhaphopsis*) *samarensis* (Vill.)		
Porthetria dispar L.	Lymantriidae	New record (USNM)
S. (*Aphantorhaphopsis*) *selecta* (Pand.)		
Paidia murina Hübner	Arctiidae	Herting, 1978:7
S. (*Aphantorhaphopsis*) *siphonoides* (Strobl)		
Delilinia pusaria L.	Geometridae	Herting, 1960:62; Mesnil, 1964: 850
Xanthorhoe biriviata Borkh.	Geometridae	Herting, 1960:62; Mesnil, 1964: 850
S. (*Baeomyia*) *juniperi* (O'Hara)		
Semiothisa trivata B. & McD.	Geometridae	O'Hara, 1984:1395
S. (*Baeomyia*) *xanthogaster* (O'Hara)		
Semiothisa sexmaculata Packard	Geometridae	O'Hara, 1984:1395
Semiothisa spp.	Geometridae	O'Hara, 1984:1395
Unidentified spp.	Geometridae	O'Hara, 1984:1395
S. (*Ceranthia*) *abdominalis* (R.-D.)		
Cosymbia annulata Schultze	Geometridae	Herting, 1960:62; Mesnil, 1963a: 841
Cosymbia orbicularia Hübner	Geometridae	Herting, 1960:62 & 1966:6; Mesnil, 1963a: 841
Cosymbia pendularia Cl.	Geometridae	Herting, 1966:6
Cosymbia porata F.	Geometridae	Herting, 1960:62 & 1966:6; Mesnil, 1963a: 841
Cosymbia ruficiliaria H.S.	Geometridae	Herting, 1966:6
S. (*Ceranthia*) *lichtwardtiana* (Villeneuve)		
Acasis viretata Hübner	Geometridae	Herting, 1966:6
S. (*Ceranthia*) *pallida* (Herting)		
Eupithecia denotata Hübner	Geometridae	Herting, 1960:62; Mesnil, 1963a: 843
S. (*Ceranthia*) *tristella* (Herting)		
Eupithecia silenata Standf.	Geometridae	Herting, 1966:6
Eupithecia undata Frr.	Geometridae	Herting, 1966:6
S. (*Pseudosiphona*) *brevirostris* Coquillett		
Oidaematophorus homodactylus Walker	Pterophoridae	Arnaud, 1978:452 (doubtful record)
S. (*Pseudosiphona*) spp.		
Chloropteryx sp.	Geometridae	New record (USNM)

Table 2 (continued)

SIPHONINE & HOST SPECIES	FAMILY	REFERENCE
Unidentified sp.	Lycaenidae	New record (USNM)
S. (Siphona) collini **Mesnil**		
Cerapteryx graminis L.	Noctuidae	Andersen, 1982:157
Euxoa temera Hübner	Noctuidae	Andersen, 1982:157
Euxoa tritici L.	Noctuidae	Andersen, 1982:157
S. (Siphona) confusa **Mesnil**		
Mythimna littoralis Curtis	Noctuidae	Andersen, 1982:157
Phlogophora meticulosa L.	Noctuidae	Andersen, 1982:157
S. (Siphona) cristata **(Fabricius)**		
Anticollix sparsata Treitschke	Geometridae	Andersen, 1982:157
Erannis defoliaria Clerck	Geometridae	Andersen, 1982:157
Antitype chi L.	Noctuidae	Andersen, 1982:157
Caradrina morpheus Hufnagel	Noctuidae	Andersen, 1982:157
Hadena bicruris Hufnagel	Noctuidae	Andersen, 1982:157
Lacanobia suasa Denis & Schiff.	Noctuidae	Andersen, 1982:157
Lacanobia oleracea L.	Noctuidae	Andersen, 1982:157
Mamestra brassicae L.	Noctuidae	Andersen, 1982:157
?Mythimna ferrago Fabr.	Noctuidae	Andersen, 1982:157
?Mythimna littoralis Curtis	Noctuidae	Andersen, 1982:157
?Mythimna obsoleta Hübner	Noctuidae	Andersen, 1982:157
?Phlogophora meticulosa L.	Noctuidae	Andersen, 1982:157
Smerinthus ocellata L.	Sphingidae	Andersen, 1982:157
S. (Siphona) geniculata **(De Geer)**		
Ceramica pisi L.	Noctuidae	Andersen, 1982:158 (doubtful record)
Tipula fulvipennis De Geer	Tipulidae	Andersen, 1982:158
Tipula lateralis Meigen	Tipulidae	Andersen, 1982:157
Tipula maxima Poda	Tipulidae	Andersen, 1982:158
Tipula montium Egger	Tipulidae	Andersen, 1982:157
Tipula oleracea L.	Tipulidae	Andersen, 1982:157
Tipula paludosa Meigen	Tipulidae	Carter *et al.*, 1981:257; Andersen, 1982:157
Tipula subnodicornis Zett.	Tipulidae	Andersen, 1982:157
Tipula vittata Meigen	Tipulidae	Andersen, 1982:158
S. (Siphona) maculata **Staeger**		
Euxoa obelisca Denis & Schiff.	Noctuidae	Andersen, 1982:157
Ochropleura candelisequa Denis & Schiff.	Noctuidae	Andersen, 1982:157
S. (Siphona) nigricans **(Villeneuve)**		
Tipula irrorata Macquart	Tipulidae	Herting, 1967a:9; Andersen, 1982:158
S. (Siphona) pseudomaculata **Blanchard**		
Faronta albilinea Hübner	Noctuidae	Blanchard, 1963:252; Guimarães, 1977:74

Table 2 (continued)

SIPHONINE & HOST SPECIES	FAMILY	REFERENCE
***S. (Siphona) setosa* Mesnil**		
Eupithecia succenturiata L.	Geometridae	Andersen, 1982:157
Allophyes oxyacantae L.	Noctuidae	Andersen, 1982:157
***S. (Siphonopsis) brasiliensis* (Townsend)**		
Rachiplusia nu Guenée	Noctuidae	Guimarães, 1977:74
Syngrapha gammoides Blanchard	Noctuidae	Guimarães, 1977:74
***S. (Siphonopsis) conata* (Reinhard)**		
Phryganidia californica Packard	Dioptidae	Arnaud, 1978:458
***S. (Siphonopsis) plusiae* Coquillett**		
Phryganidia californica Packard	Dioptidae	Arnaud, 1978:458
Autographa californica Speyer	Noctuidae	Arnaud, 1978:459
Trichoplusia ni Hübner	Noctuidae	Arnaud, 1978:459
Unidentified spp.	Noctuidae	Arnaud, 1978:459
***Siphona s. l.* (New World) sp. 7**		
Cladara limitaria Walker	Geometridae	New record (CNC)
Stenoporpia sp.	Geometridae	New record (CNC)
Panthea portlandia Grt.	Noctuidae	New record (CNC)
***Siphona s. l.* (New World) sp. 8**		
Ectropis crepuscularia Denis & Schiff.	Geometridae	New record (CNC)
Epirrita autumnata Bkh.	Geometridae	New record (CNC)
Melanolophia imitata Walker	Geometridae	New record (CNC)

EVOLUTION OF THE SIPHONINI

Introduction

Many methods are presently available for inferring phylogenies through cladistic analyses, but most are theoretically similar in that they begin with polarization of character states into plesiotypic (ancestral) and apotypic (derived), generally based on an outgroup comparison. Taxa are then ordered into a hierarchy of nested sets (a cladogram) on the basis of synapotypic (shared derived) states. General methods of phylogenetic analysis are described by Wiley (1981) and are under constant review and refinement in the pages of *Systematic Zoology*.

Polarization of character states in the Siphonini is not possible for many of the characters given in the Structural Features chapter. One of the problems is the uncertainty regarding the sister group to the Siphonini. This problem required that the outgroup comprise a selection of species from several tachinid tribes of possible close relationship to the Siphonini. Names of species selected for this purpose are listed in Table 3 along with their geographic distribution. Such an extended outgroup was useful for detecting and dismissing many very homoplastic states from the phylogenetic analysis, but also required the rejection of possibly useful states which might have been phylogenetically interpretable if tribal relationships between the Siphonini and the extended outgroup were better resolved. A preliminary analysis of the phylogenetics of the Siphonini established *Siphona s.l.* as a monophyletic clade within the tribe, so non-*Siphona s.l.* siphonines were considered the functional outgroup (Watrous and Wheeier 1981) for polarization of states among *Siphona s.l.* subgenera.

Character weighting is a controversial subject because any system of weighting is subjective in practice, yet equal weighting of all apotypic states is even more undesirable because a simple tally of apotypic states does not recognize the fundamental value of evolutionary novelty and complexity in phylogenetic reconstruction.

A very simple approach to character weighting has been adopted here. Two levels of synapotypy are recognized - primary and secondary. A primary synapotypy is one founded on state complexity and a minimum of homoplasy within both outgroup and the Siphonini. A secondary synapotypy is usually structurally less complex and/or more homoplastic than a primary synapotypy, or the character has been insufficiently studied for the apotypic state to be hypothesized as a primary synapotypy at this time.

Primary and secondary synapotypies of the Siphonini provide good evidence for the monophyly of most siphonine genera and subgenera but resolve few intergeneric, or *Siphona s.l.* intersubgeneric, relationships (Fig. 164).

The synapotypies for siphonine genera and subgenera are discussed under the Phylogenetics section of each taxon in the Classification chapter. They are summarized below and designated as primary or secondary, and incidents of homoplasy are noted. Many characters of the Structural Features chapter are deemed

unsuitable for phylogenetic analysis so the numbers below do not correspond to those in that chapter. Similarly, certain states are defined differently below than in the Structural Features chapter so a direct correlation is not possible between the states in both sections. Characters and states of the Structural Features chapter that are the same as those discussed here are indicated below in square brackets. The three species groups of undescribed *Siphona s.l.* are considered inadequately studied to include under the discussion of primary and secondary synapotypies.

Intergeneric relationships of non-*Siphona s.l.* siphonines and intersubgeneric relationships of *Siphona s.l.* are not interpretable by primary or secondary synapotypies except for the *Proceromyia-Entomophaga* lineage. However, the distribution of certain, less reliable, states suggest possible higher relationships within these groups, and these possibilities are explored at the end of this section and depicted in Figs. 166-171.

Monophyly of the Siphonini

1P. The best supported synapotypy of the Siphonini is the presence of only two spermathecae in the reproductive system of adult females. This synapotypy was proposed by Andersen (1983) in his revision of the Old World Siphonini, and is supported here by its universality among all female siphonines dissected during this study (comprising approximately 90 species, or almost 25% of the known described and undescribed siphonine species). Only species of the unrelated Neotropical genus *Phaenopsis* Townsend are known to share this state within the Tachinidae (Andersen 1983).

2P. The pregonite of adult male siphonines is membranous anteriorly from its apex to its basal articulation with the hypandrium (Figs. 71-106; universal among dissected males of over 250 siphonine species). According to Tschorsnig (1985 and pers. comm.), this state is unique to the Siphonini, with other tachinids lacking membrane in this position. Based on Tschorsnig's findings, the state in the Siphonini is tentatively proposed as a synapotypy of the tribe.

3S. Possibly synapotypic of the Siphonini is absence of accessory glands from the reproductive system of adult males. This synapotypy was suggested by Andersen (1983), based on examination of dissected males of a limited number of Old World siphonine species. Andersen noted that male accessory glands are absent from several other, apparently unrelated, tachinids. This synapotypy is in need of corroboration because it is based on few representatives of the Siphonini and was not investigated during this study.

Andersen (1983) also proposed that convergent subapical setae on the scutellum are synapotypic of the Siphonini. This state is shared with possible sister groups to the Siphonini (in particular some species of the Leskiini and Clausicellini) and therefore cannot be defended as synapotypic of the tribe at this time.

Book Review

Table 3. Tachinid species examined for outgroup comparison with the Siphonini.

TRIBE AND SPECIES	DISTRIBUTION
Ernestiini	
Eloceria delecta (Meigen)	Europe
Synactia parvula (Rondani)	Europe
Triarthriini	
Triarthria setipennis (Fallén)	Europe
Aphriini	
Aphria ocypterata Townsend	Nearctic
Solieria pacifica (Meigen)	western Palearctic
Solieria sp.	Arizona (USA)
Leskiini	
Atylostoma towadensis (Matsumura)	eastern Palearctic & SE Asia
Drepanoglossa lucens Townsend	Nearctic
Genea brevirostris (James)	eastern Nearctic
Genea texensis (Townsend)	Nearctic
Genea robertsonii (Townsend)	southern Nearctic
Leskia aurea (Fallén)	Palearctic
Leskia depilis (Coquillett)	eastern Nearctic
Leskia sp.	New Mexico (USA)
Trochiloleskia loriola (Reinhard)	southern Nearctic
Clausicellini	
Clausicella sp.	Arizona (USA)
Crocinosoma cornuale Reinhard	southern Nearctic
Dolichopalpellus mirabilis Townsend	SE Brazil
Epicoronimyia mundelli (Blanchard)	Argentina & Chile
Ginglymia acirostris Townsend	Nearctic
Ginglymia johnsoni (Coquillett)	Nearctic
Phantasiomyia sp.	California (USA)
Spathipalpus philippi Rondani	Argentina & Chile
Neaerini	
Camposodes evanescens Cortés	Chile
Neaera laticornis (Meigen)	Palearctic
Neaera leucoptera (Johnson)	central and eastern Nearctic
Neaera robertsonii (Townsend)	central and eastern Nearctic
Phytomyptera setigera (Thomson)	western Nearctic
Phytomyptera sp.	Arizona (USA)

Monophyly of genera and subgenera

Synapotypies of the genera and subgenera of the Siphonini are summarized below. Most are discussed in more detail in the Phylogenetics section of each genus and subgenus.

Goniocera Brauer and Bergenstamm

4P. *Goniocera* species are unique among siphonines in having a row of *ad* setae on the mid tibia. This state is shared with a few species in the outgroup, but most outgroup species have one seta in this position. This latter state is probably in the groundplan of both the outgroup and the Siphonini. [Character 24.]

5P. Known hosts are larvae of *Malacosoma* species (tent caterpillars), a parasitic habit unique to this genus (host of *G. montium* unknown).

6S. Median lobe of male sternum 5 prominent and flattened on posteromedial surface (Fig. 47; *G. montium* not examined). This state is approached in a few other siphonines and similar in a few *Ceromya s.s.* species, but is probably independently derived in *Goniocera*. [Character 40, state **F**.]

7S. Posterolateral margin of distiphallus curved inward toward midline and slightly incised from rest of lateral surface (not visible in Fig. 107 and not examined in *G. montium*). This state is only known to be shared with *Ceromya flaviseta* and *C. ontario*, but other characters do not support a close relationship between these species. [Character 49, state **S**.]

8S. Female sternum 8 reduced in size (Fig. 145). This state is not considered a primary synapotypy because the female genitalia of two of the four species, *G. montium* and *G. versicolor*, were not examined. [Character 62, state **R**.]

9S. Male surstylus narrowly fused basally with the epandrium (Fig. 137, not examined in *G. montium*). This state is common in many *Ceromya* species but few other siphonines, so may be independently derived in *Goniocera*. [Character 52, state **F**.]

10S. Male cerci sharply inflexed at midpoint and densely setose on basal half (Fig. 137, not examined in *G. montium*). Like the former character, this condition of the cerci in *Goniocera* species is shared with many *Ceromya* species and a few other siphonines. [In part, character 54, state **I**.]

Proceromyia Mesnil

11P. Distiphallus in lateral view with long, broad, anteriorly spined, anterolateral arm and short lateral projection (Figs. 108-109). Shape of the distiphallus is closely approximated only in the hypothesized sister group, *Entomophaga* (Figs. 110-111).

12P.   Male sternum 5 (Figs. 48-49) with apical lobe slightly differentiated [character 38, state **O**] and median lobe slightly sinuous and rounded [character 40, state **R**].

13P.   Head with narrow vertex (Mesnil and Shima 1978: 325).

14P.   Large tarsal claws. This state is also present in a few *Siphona s.s.* species, though certainly independently evolved in that group. [Character 26, state **L**.]

15S.   A possible synapotypy is the bare prosternum. This state is shared with *Ceromya monstrosicornis*, some specimens of *Goniocera io* and a few other siphonines. Setulation on the prosternum is a difficult character to polarize because it is obviously very homoplastic. A bare prosternum predominates in the outgroup, but some species of the Clausicellini and Neaerini have a setulose prosternum. The latter state is almost universal among siphonines, but particularly for two reasons - its presence in *Entomophaga* (the hypothesized sister group to *Proceromyia*), and its requirement of fewer reversals - a setulose prosternum is here considered the more likely groundplan state of the Siphonini.

Entomophaga Lioy
16P.   Aristomere 1 elongate, at least 1.5X longer than wide (Figs. 4-5). This state is also independently derived in a few *Siphona s.l.* species. [Character 9, state **L**.]

17S.   The general habitus of the two *Entomophaga* species, particularly with respect to head features (Figs. 4-5; small eye, similar-shaped flagellomere 1) suggests they are sister species.

18S.   Female sternum 8 is absent from *E. nigrohalterata* (Fig. 147). If similarly absent from the female of *E. exoleta*, then this condition would represent a primary synapotypy.

Ceromya s.l. Robineau-Desvoidy
19S.   It is not possible to cite a single state which is synapotypic of *Ceromya s.l.* species, yet *Ceromya s.s.* and the *C. silacea* species group are probably each monophyletic and have certain features in common which attest to their close evolutionary grade if not strict monophyly. These include the diagnostic features of *Ceromya s.l.* given in the Classification chapter as well as the following features of the male genitalia shared by some but not all species of both subgroups (and a few other siphonines, most notably *Goniocera* species (Fig. 137), the significance of which is discussed later in this chapter): surstylus basally fused with epandrium [character 52, state **F**], cerci sharply inflexed at midpoint [character 54, state **I**] and densely setose on basal half (Fig. 138). All the above states are grouped together here as a secondary synapotypy of *Ceromya s.l.* because they may be

phylogenetically important even though they do not clearly establish the monophyly of the genus.

Andersen (1983) proposed as a synapotypy of *Ceromya s.l.*: "Praegonite oval with the sclerotized part more or less bilobed and recurved" (p. 12). Shape of the sclerotized portion of the pregonite is more varied than suggested by Andersen and is therefore not considered a synapotypy here. However, the oval shape is attributable to the enlarged membrane anteriorly, and this is here considered a synapotypy of *Ceromya s.s.*

Ceromya s.s. Robineau-Desvoidy
20P. Features of the pregonite provide the only convincing synapotypy of this group. The membrane anteriorly on the pregonite is characteristically enlarged and in most species spinulose (Figs. 39-40, 77-83). (The spinules are very tiny in some species and consequently have been overlooked by previous workers.) Almost all *Ceromya s.s.* species examined and lacking spinules on the pregonite are assignable to species groups which possess them, so this state is considered that of the groundplan of *Ceromya s.s.* The phylogenetic significance of similar spinules on the pregonite of *Goniocera io* is discussed later in this chapter. [Character 45, state **M**.]

Ceromya Nepal sp. 1 and *C. monstrosicornis* are tentatively included in *Ceromya s.s.* until their phylogenetic position is better resolved (see Phylogenetics section of *Ceromya s.s.*).

Ceromya silacea species group
21P. Distiphallus with internal sclerotized structure, which is continuous with infolded posterior margins (Fig. 112). This structure is unique to members of the *C. silacea* species group.

22S. The first instar of *C. silacea* has a hook-like labrum (Fig. 159). This is proposed only tentatively because first instars of other members of this group have not been examined.

The phylogenetic history of *Ceromya s.l.* is not clearly understood. The present division of the genus into *Ceromya s.s.* and the *C. silacea* species group is based on male genitalic states, and may be incomplete until males of all described *Ceromya* species are examined. It seems premature to erect a new subgenus for the *C. silacea* species group until the phylogenetics of the genus are better understood. Recognition of two subgenera must await corroboration of *Ceromya s.s.* and the *C. silacea* species group as monophyletic lineages and sister groups.

Actia Robineau-Desvoidy
23P. Male pregonite (Figs. 41-42, 85-86) approximately J-shaped [character 44, state **J**] and spinose [character 45, state **S**].

24P. *Actia* species, with few exceptions, possess a row of hairs on the katepisternum anterior to the mid coxa (Fig. 33). This state is unique to *Actia* species and *Entomophaga exoleta* among siphonines, though is also present in some species of the outgroup. No evidence suggests that *Actia* is the primitive lineage of the Siphonini so presence of a katepisternal row of hairs is hypothesized as synapotypic of *Actia* species. The same state in *E. exoleta* is hypothesized as independently derived. [Character 20, state **S**.]

25P. An approximately V-shaped sternum 5 with an indistinct median lobe (Figs. 58-59) is apparently the groundplan state of the genus and approximated by few other siphonines. [Character 38, state **V** and character 40, state **U**.]

26S. Almost all *Actia* species have two setulae on the upper portion of the anepisternum (Fig. 31), whereas one setula is found in most other siphonines (Fig. 32) and is almost universal in the outgroup. This state is weighted as a secondary synapotypy because it is widely distributed throughout different siphonine lineages even though present in relatively few non-*Actia* species. [Character 19.]

27S. The lack of a dorsal cornu in the cephalopharyngeal skeleton of first instars of examined *Actia* species is certainly apotypic (Fig. 160), but the universality of this state throughout the genus needs to be investigated (see O'Hara in press "a"). [Character 65, state **A**.]

Peribaea Robineau-Desvoidy
28P. A strong, downwardly directed, proepimeral seta (Fig. 27) is shared by all known *Peribaea* species and absent from other siphonines. Most neaerines and some other tachinids also share this state, but are not closely related to *Peribaea*. [Character 18, state **P**.]

29P. Distiphallus sclerotized posteriorly (partially unsclerotized [incised] in all but three other examined and unrelated siphonine species). Andersen (1983) considered *Peribaea* to be the most primitive lineage of the Siphonini and a posteriorly sclerotized distiphallus both plesiotypic and the groundplan state in the tribe. My outgroup comparison does not support this polarization (*i.e.* nothing comparable to the *Peribaea* condition was found in the outgroup) and I place *Peribaea* near *Siphona* based on characters discussed below. [Character 48, state **E**.]

30P. Females of most *Peribaea* species have a distinct sternum 8, though bare as compared with haired as in other siphonines. The female ovipositor is elongate and sternum 8 lacking in a few highly derived *Peribaea* species. [Character 62, state **B**.]

31S. First instars with narrowed, and in most species hook-like, labrum (Fig. 161). Outgroup comparison is not helpful in the polarization of this state because both a

hook-like and hatchet-like labrum are widely distributed throughout the Tachinidae. Andersen (1983) interpreted *Peribaea* as primitive and a hook-like labrum as plesiotypic, but this state is more likely apotypic if the present phylogenetic placement of *Peribaea* is correct. [Character 64, state **N**.]

Siphona Meigen *sensu lato*
32P. First instars with from two to a row of large spinules or hooks on the posteroventral margin of segment 6 (Figs. 162-163), with the exception of *S. (Aphantorhaphopsis)* Uganda sp. 1. Except for *Ceromya* Australia sp. 3, non-*Siphona* species have tiny spinules or are bare in this position (Figs. 158-161). [Character 66.]

33P. First instars, with few exceptions, with single dominant row of spinules on the posteroventral margin of segment 7. Almost all examined first instars of non-*Siphona* species have two or more rows of spinules or spines in this position [Character 67, state **S**; refer to figure numbers cited therein.]

The Old World component of *Siphona s.l.*, comprising the subgenera *Aphantorhaphopsis*, *Ceranthia* and *Siphona*, was interpreted as monophyletic by Andersen (1983) based on two hypothesized synapotypies. One was presence of an anterior apodeme on female sternum 7, which is correctly polarized as apotypic in the Siphonini based on outgroup comparison. However, this state is widely distributed throughout the tribe (see Table 1) and therefore too homoplastic to interpret as a synapotypy of *Siphona s.l.* [character 58, state **W**]. The second state that Andersen considered synapotypic of Old World *Siphona s.l.* was presence of a long lower katepisternal seta. I interpret this state differently from Andersen, as discussed under the section on monophyly of *Peribaea* and *Siphona s.l.*

Siphona (subgenus *Actinocrocuta* Townsend)
34S. Pregonite (Fig. 89) very slender and elongate [character 44, state **A**], with outer surface short spinose apically [character 45, state **T**].

35S. Distiphallus slender and parallel-sided (Figs. 122-123).

36S. Cerci in posterior view broadened to near apex (Fig. 142).

The above states are individually present in a few other siphonines but the combination of all three is unique to this subgenus and none appear to be synapotypic between *S. (Actinocrocuta)* and another *Siphona* subgenus.

Siphona (subgenus *Aphantorhapha* Townsend)
37S. Distiphallus tapered to a rounded or pointed tip (Fig. 124).

38S. Cerci broadened at midlength in posterior view (Fig. 143). The cerci of *S. (Aphantorhapha) atoma* do not share this apotypy and may be plesiotypic in this respect, though other states support a sister group relationship between this species and *S. (Aphantorhapha) arizonica*.

Siphona (subgenus *Aphantorhaphopsis* Townsend)

This taxon is non-monophyletic and comprises all Old World *Siphona s.l.* species not assignable to *S. (Siphona)* or *S. (Ceranthia)*. The included species are too inadequately known to be reclassified into monophyletic lineages at this time. None of the examined species appears to belong in the otherwise strictly New World supraspecific taxa of *Siphona s.l.*

Siphona (subgenus *Baeomyia* O'Hara)

39P. Mid tibia without an *ad* seta near midlength (Fig. 38). Species of this subgenus are not closely related to the few other siphonines with this state. [Character 24.]

40P. Aristomere 1 very elongate, at least 2X longer than wide (Fig. 15). This state is independently derived in a few other, unrelated, siphonines. [Character 9, state **L**.]

41P. Adults are the smallest of siphonines, with a total length of 2.0-3.0mm. Few other siphonines are typically as small; the average length of adults in other lineages is 3mm or longer. [Character 1.]

42P. Aristomere 3 very short (Fig. 15). [Character 11, state **V**.]

43S. Crossvein *dm-cu* far removed from wing margin (Fig. 22). This state is also found in a few other siphonine lineages, and may not be synapotypic of *S. (Baeomyia)* species. However, the state is obviously homoplastic so is not used here to define a higher subgroup within *Siphona s.l.* [Character 34.]

Siphona (subgenus *Ceranthia* Robineau-Desvoidy)

44P. Adults with cylindrical palpus (Fig. 16). This feature is considered independently derived in two species of *S. (Aphantorhaphopsis)*. [Character 14, state **C**.]

45P. Pregonite with long seta posteriorly (Fig. 94). The bare state of the pregonite in *S. (Ceranthia)* Mauritius sp. 1 is interpreted as autapotypic. [Character 46, state **L**.]

46P. Distiphallus with short to long posterolateral arm which is distinctly incised from rest of lateral surface (Fig. 127). The characteristic shape of the distiphallus in *S. (Ceranthia)* species is at least subtlely different from other siphonines which also

possess distinct posterolateral projections. [Character 49, states **M** and **E.**]

Siphona (subgenus *Pseudosiphona* Townsend)

47P. Pregonite (Fig. 95) broadened in lateral view [character 44, state **W**], with spinules anterolaterally [character 45, state **T**] and two to several tiny setae posteriorly [character 46, state **F**]. Few *S. (Pseudosiphona)* species lack one or another of these states, but other siphonines do not possess more than one.

48P. Distiphallus triangular and anterolaterally spined (Fig. 128). This state is interpreted as that of the groundplan in this subgenus, and the few species which depart from it are regarded as apotypic in this respect.

49S. Labrum of first instars elongate and hook-like in most species (Fig. 162). Species of *S. (Pseudosiphona)* with a more broadened labrum seem derived from other species in which the labrum is hook-like. Shape of the labrum is a somewhat homoplastic character so this state is ranked as a secondary synapotypy. [Character 64, state **N.**]

50S. The groundplan condition, and possible synapotypy of this subgenus, is moderately lengthened labella (slightly longer than half prementum length; Fig. 17). [Character 16, state **M.**]

Siphona (subgenus *Siphona* Meigen *sensu stricto*)

51P. Proboscis with elongate prementum and labella, with latter at least as long as the former (Figs. 25-26). This state is present in all *S. (Siphona)* species, and convergently present in some other siphonines. [Character 16, state **L.**]

52S. The male genitalia of *S. (Siphona)* species are remarkably homogeneous for such a large group of species. There is relatively little variation in shapes of pregonite (Fig. 96), surstylus and cerci (Figs. 141, 144), while differences in distiphallus shape (Fig. 129) are more conservative than in any other large siphonine taxon. Perhaps in combination, these features of the male genitalia can be considered synapotypic of the subgenus, though individually none is unique.

Siphona (subgenus *Siphonopsis* Townsend)

53P. Distiphallus tapered to a narrow and truncate tip of varied length (Fig. 130). This state is evidently unique to *S. (Siphonopsis)*.

54S. Labellar length characteristically slightly less than three-fourths prementum length (Figs. 18, 24). This length is not unique to, but is probably synapotypic of, the subgenus. [Character 16, state **E.**]

Siphona (subgenus *Uruactia* Townsend)

55P. Distiphallus in profile smoothly tapered and apically pointed (Fig. 131). *S. (Aphantorhapha)* species are characterized by a somewhat similar-shaped distiphallus.

There are only two species included in *S. (Uruactia)*, and these are easily recognized as sister species because of several similarities, but each shared state is too widely distributed among other siphonine species to be included here.

Monophyly of the *Proceromyia* Mesnil and *Entomophaga* Lioy lineage

56P. Distiphallus of all four described species characterized by long, spined, anterolateral arm and incised lateral surface (Figs. 108-111). No examined outgroup species or other siphonine has very similar distiphallus features.

57P. Pregonite smoothly curved and apically pointed, with longitudinal ridge which is bare or spined (Figs. 73-76). A spined longitudinal ridge is also present in a few New World *Siphona s.l.* species, but the shape of the pregonite is different (Figs. 103-105) and other character states (for example, presence of a seta posteriorly on pregonite as in Figs. 103-104) clearly indicate that these species are not closely related to the *Proceromyia-Entomophaga* lineage. [Character 45, state **L.**]

Monophyly of the *Peribaea* R.-D. and *Siphona* Meigen lineage

58P. Anal vein extended to wing margin at least as fold (Fig. 22). The groundplan state for the Tachinidae and presumably the Siphonini is anal vein not extended to wing margin. This state in three species of *Actia* is interpreted as independently derived. Andersen (1983) considered *Peribaea* the primitive lineage of the Siphonini and accordingly interpreted anal vein reaching wing margin as synapotypic of the Siphonini and anal vein not reaching wing margin as an apotypic loss in his *Actia* group (*Goniocera*, *Ceromya* and *Actia*). [Character 33, state **E.**]

59P. Lower katepisternal seta subequal in length to, or longer than, upper anterior seta (Fig. 32). The near universality of this state within this lineage compared with a shorter lower seta in the outgroup and almost all other siphonines is good evidence that this state is synapotypic of this lineage. Andersen (1983) also polarized a long lower katepisternal seta as apotypic, but interpreted the apotypic state in a more restricted sense. He considered the state in which this seta is longer than the upper anterior seta as synapotypic of Old World *Siphona s.l.* (his *Asiphona*, *Ceranthia* and *Siphona*). This state is the most common among species of world *Siphona s.l.*, but the lower and upper anterior setae are subequal in length in species of some lineages (Table 1). The subequal condition of these setae is found in the majority of *Peribaea* species and is here interpreted as the groundplan state of the *Peribaea-Siphona s.l.* lineage because a short lower seta characterizes all other siphonine lineages. [Character 21, states **E** and **L.**]

Phylogenetics of non-*Siphona s.l.* siphonine lineages

There are no convincing synapotypies among non-*Siphona s.l.* genera of the Siphonini except those already discussed for the *Proceromyia-Entomophaga* lineage. As equivocal as the generic relationships may be, two characters warrant discussion because the interpretation of their states suggest different phylogenetic scenarios concerning the evolution of *Goniocera*. (No phylogenetic statements about the interrelationships of *Actia*, *Ceromya s.l.* and the *Proceromyia-Entomophaga* lineage are made at this time because no shared states which are phylogenetically interpretable were found among these taxa.)

Goniocera is well established as a monophyletic taxon of the Siphonini (Fig. 164), but its phylogenetic position within the tribe can be interpreted in several ways depending upon the polarization of the states of two characters: (1) length of preapical *ad* seta on fore tibia [character 23], and (2) presence or absence of spinules on the membranous portion of male pregonite [character 45]. The distribution of states for these characters among the four *Goniocera* species and major lineages of the Siphonini is shown in Fig. 165, without polarization of states into plesiotypic and apotypic. The states of three other characters important to the discussion of the phylogenetics of *Goniocera* are also included in Fig. 165.

Length of the preapical *ad* seta on the fore tibia is a difficult character to polarize into plesiotypic and apotypic states. Several species of the outgroup (both species of the Ernestiini, *Triarthria setipennis* and *Neaera robertsonii*; Table 3) have an *ad* seta subequal in length to the preapical *d* seta, but in the others it is short. The character is also varied among siphonines, as documented in Table 1 and Fig. 165, so reversals have presumably taken place in both the outgroup and the Siphonini. Yet a possibility is raised that needs to be investigated further: perhaps the presence of a long preapical *ad* seta in some *Goniocera* species and the four species of *Proceromyia* and *Entomophaga* represents a synapotypy of these three genera, with a reversal within *Goniocera* and independent acquisitions of the state in two species of *Ceromya s.s.*[7], several *Actia* species and one species of *S. (Aphantorhaphopsis)*. This scenario is illustrated in Fig. 166. The evidence for this interpretation is very weak, though it is worth noting that the members of these three genera are also similar in appearance, with mostly dark coloration and non-vittate, uniformly pruinose abdomens. Are the long preapical *ad* seta and similar appearance of these taxa indicative of their common ancestry, their primitiveness among siphonines, or the result of frequent homoplasy and hence of little value in phylogenetic reconstruction? The evolutionary history of *Goniocera* is far from clear because the states of the second character to be discussed are non-congruent with any but the last interpretation.

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[7] the presence of this state in two *Ceromya s.s.* species is discussed in the Phylogenetics section of *Ceromya s.s.*

Considerable weight is placed here upon the presence of spinules on the membranous portion of the male pregonite being an apotypic state [character 45, state M]. This state is considered synapotypic of *Ceromya s.s.* for the reasons discussed in the Phylogenetics section of that taxon. As shown in Fig. 165, this state is also found in *Goniocera io* and apparently nowhere else in the Siphonini. The distribution of this apotypic state can be interpreted in many ways, of which three seem more reasonable than the rest: (1) the state arose independently (and convergently) in *G. io* and *Ceromya s.s.* (Fig. 167), (2) the state arose once, and *Goniocera* and *Ceromya s.s.* are sister groups (with subsequent reversals within both taxa; Fig. 168), or (3) the state arose once, and *Goniocera* is a derived subgroup of *Ceromya s.s.* (Fig. 169).

Under the first of the above interpretations (illustrated in Figs. 164 and 167), no sister group relationship is indicated between *Goniocera* and another siphonine taxon. Under the next two interpretations (illustrated in Figs. 168 and 169, respectively), the apotypic state is considered synapotypic of *Goniocera* and *Ceromya s.s.* and differ only with respect to the monophyly of *Ceromya s.s.*

The hypothesis of *Goniocera* and *Ceromya s.s.* sharing a common ancestry at first seems highly improbable, for it requires loss of spinules from the pregonite of all *Goniocera* species except *G. io* as well as loss in many *Ceromya s.s.* species (or non-expression of the apotypic state if it is interpreted as an underlying synapotypy[8]). There is reason to believe that the apotypic state is the groundplan state of *Ceromya s.s.* (as discussed in the Phylogenetics section of that taxon), but not convincingly (or even probably) for *Goniocera*. Nevertheless, the cladograms pairing *Goniocera* and *Ceromya s.s.* (Figs. 168-169) are presented as alternative (and testable) hypotheses because monophyly of *Goniocera+Ceromya s.s.* would help explain the distribution of three other male genitalic character states. The three characters are shape of median lobe on sternum 5, articulation between surstylus and epandrium, and shape of cerci in profile; the distribution of their states is shown in Fig. 165 (along with the states for the two characters discussed above). If the solid dots are interpreted as apotypic states, then these are present in all examined *Goniocera* species and at least some species of *Ceromya s.s.* and the *C. silacea* species group. Decreasing the probability of a close relationship between *Goniocera* and *Ceromya* is the possibility of the three states being primitive, the possibility of homoplasy (note the presence of these states in a few other siphonines), and the fact that the three states are not all present in any *Ceromya s.s.* species.

In summary, the · phylogenetic position of *Goniocera* among non-*Siphona* siphonines remains enigmatic, with a possible close relationship being indicated between it and the *Proceromyia-Entomophaga* lineage (Fig. 166) or *Ceromya s.s.* (Figs. 168-169). Since both these interpretations are highly speculative, the polychotomus (and unresolved) depiction of the origin of *Goniocera* in Fig. 164

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[8]underlying synapotypies are discussed in the next section.

(and Fig. 167) is that best reflecting the current state of knowledge of this problem.

Phylogenetics of *Siphona* subgenera

Nine subgenera of *Siphona s.l.* are recognized, with all but *S. (Aphantorhaphopsis)* hypothesized as monophyletic (Fig. 164). No clear synapotypies were found between subgenera, though three derived character states which are widely distributed among the subgenera provide some information about possible higher groupings within the genus and weak additional support for its monophyly. These character states, all belonging to characters of the male genitalia, are reviewed below and their phylogenetic significance discussed.

The least informative of the three states concerns shape of the apex of the apical lobe on abdominal sternum 5 [character 39]. As documented in Table 1, the tip of the apical lobe is curved inward in at least some members of most *Siphona* lineages (state C), yet this state is virtually absent from other siphonines (observed in only one *Ceromya s.s.* species). The distribution of state C in the Siphonini suggests that this state is apotypic within *Siphona*, but note that nine of the ten *Siphona* taxa with state C in Table 1 also have state A (apical lobe not curved inward at apex; plesiotypic). This character state distribution may be the result of one or more of the following: (1) homoplasy, possibly resulting from parallel selection (as defined below), (2) reversals to state A from groundplan (and apotypic) state C (also a type of homoplasy, though groundplan state different from that of previous explanation), and/or (3) an underlying synapotypy (as defined below). It is unlikely that the first type of homoplasy alone could account for such a wide distribution of state C among *Siphona* lineages. Equally unlikely is the interpretation of state C as the groundplan state of most *Siphona* lineages with subsequent reversals in almost all lineages. (The groundplan state is clearly A in at least *S. (Siphona)*, as only three unrelated species of the 40-odd species examined for this character possess state C.)

Saether (1979: 305) recognizes two types of parallelisms: (1) "parallelism as a result of *parallel selection* influencing homologous structures" and (2) "parallelism as the result of common inherited genetic factors including parallel mutations, i.e. *underlying synapomorphies*". An underlying synapomorphy (or more generally, synapotypy) has also been described by Saether as "the capacity or tendency to develop parallel similarity" (1977: 31). I suspect that the inwardly curved apical lobe on male sternum 5 results from one of these forms of parallelism, for neither homoplasy nor state reversals provide as satisfactory an explanation for the presence of both states A and C in nine of 13 *Siphona* taxa listed in Table 1. It is not so clear which form of parallelism the shape of the apical lobe is governed by, yet this is the key to its interpretation since, as Saether comments, "parallel selection is of no greater value than convergence, while underlying synapomorphy is comparable to true synapomorphy" (1979: 306). Perhaps there is an inherent tendency (=underlying synapotypy) among most *Siphona* lineages to develop an inwardly curved apical lobe. This would explain both the near ubiquity of state C throughout

Siphona lineages and its virtual absence from other siphonines. Yet the character in question is also one in which the difference between one state (**A**) and another (**C**) involves little change, and the taxa grouped by the presence of the apotypic state seem subjectively no more phylogenetically significant than the polychotomy depicted in Fig. 164. Several factors, including the following, may be involved in expression of state **C**, all of which contribute to my interpretation of this state as a non-informative apotypic state: (1) state **C** is not complex so homoplasy may be involved to some degree, (2) there may be a selective advantage to state **C** which would therefore reduce its phylogenetic value, and (3) *Siphona* lineages from which state **C** is unrecorded may nevertheless possess the underlying synapotypy.

Two states of the male pregonite are interpreted as apotypic within *Siphona s.l.* because they are absent from all other siphonines. One is presence of spinules on the distal portion of the pregonite [character 45, state **T**], which is restricted to New World *Siphona* species of subgenera *Actinocrocuta* (Fig. 89) and *Pseudosiphona* (Fig. 95), some members of New World species groups 1 (Fig. 100) and 2, and several unplaced New World *Siphona s.l.* species (Table 1). The other state, presence of a seta posteriorly on the pregonite [character 46, states **T**, **M**, **L**, **F**; figures numbers for each state listed in Structural Features chapter], is more widely distributed throughout *Siphona s.l.*, and only unrecorded from subgenera *Siphona* and *Uruactia* (Table 1).

The apotypic states of both pregonite characters are regarded as underlying synapotypies (as defined above) because each involves a novel and complex feature that almost certainly would not arise convergently, nor doubtfully by parallel selection, among so many different lineages. As with the sternum 5 character, some lineages with an apotypic state of the pregonite also have species with a plesiotypic state, so the term underlying synapotypy is preferable to synapotypy, and arguably more correct than postulating a synapotypic groundplan state followed by numerous reversals. The difference in interpretation between the apotypic states of the pregonite and state **C** of the apical lobe of sternum 5 is primarily due to the greater complexity of the former, though as will become apparent other difficulties in interpretation remain the same. Each pregonite character will be discussed in turn, beginning with the setal character.

A seta posteriorly on the pregonite is a widely distributed, apotypic state among *Siphona s.l.* lineages, though is absent from one or more species of most of these lineages (Table 1). It is particularly evident that lineages in which most species have a tiny seta also have species which lack it, so to some extent there seems to be a graded potential for development of a pregonite seta among *Siphona* lineages (with a large seta almost unique to, and hypothesized as a synapotypy of, *S. (Ceranthia)*). One of the difficulties in interpretation of an underlying synapotypy is how to infer its presence or absence in a taxon from which the apotypic state is unrecorded. Certainly there is no reason to suppose that a pregonite seta is an underlying synapotypy of any non-*Siphona* siphonines, but how does one interpret the absence

of the apotypic state in subgenera *Siphona* and *Uruactia*? Only two species of *S. (Uruactia)* are known, and male genitalia of only two specimens were examined, so these findings provide only weak (and inconclusive) evidence for the lack of the underlying synapotypy in this subgenus.

The situation is different for *S. (Siphona)*, as male genitalia of nearly 40 species of this diverse subgenus were examined, and none possess a seta posteriorly on the pregonite. These findings are far from conclusive, but they are suggestive of *S. (Siphona)* occupying a rather primitive position among *Siphona s.l.* lineages. This interpretation is neither supported nor refuted by other characters at this time. It might be argued that a primitive position within *Siphona s.l.* is consistent with the speciose nature and wide geographic distribution of the subgenus, but the conservative features of its many members do not preclude a more recent and rapid radiation of the taxon.

Even if one considers *S. (Siphona)* as a rather primitive lineage of *Siphona s.l.*, it is doubtfully the *most* primitive. That position probably belongs to certain members of the Old World (probably polyphyletic) taxon *S. (Aphantorhaphopsis)*. This subgenus includes species with or without a pregonite seta, and it is possible that some of the latter represent the most primitive lineages of *Siphona s.l.* This interpretation is illustrated in Fig. 170, with *S. (Siphona)* shown in a primitive position relative to most other subgenera, and *S. (Uruactia)* questionably placed near *S. (Siphona)*. Fig. 170 represents one of the more parsimonious interpretations of the character under discussion, though it must be noted that it is presented as a hypothetical model to be tested, and not as a well corroborated cladogram.

I return now to a consideration of the phylogenetic significance of the field of spinules distally on the sclerotized portion of the pregonite of *S. (Actinocrocuta)* and *S. (Pseudosiphona)* species, some species of New World species groups 1 and 2, and some unplaced New World *Siphona s.l.* species (Table 1 - character 45, state **T**). Much of the discussion above concerning the pregonite seta applies here as well, as a field of spinules is interpreted as an underlying synapotypy of those taxa in which the state is both present and absent. A cladogram based strictly upon the criterion of presence of the apotypic state in at least one species of a *Siphona* lineage is shown in Fig. 171, but again it must be cautioned that non-expression of this underlying synapotypy in taxa grouped on the left side of the cladogram would lead to misinterpretation of the phylogenetic affinities among these taxa. Of significance is the fact that all taxa grouped by presence of the spinulose state are New World in distribution, and there almost entirely restricted to the tropics and subtropics. Whether or not one or more of the other New World taxa belong in this group, there is at least evidence here for evolution of a higher clade of *Siphona s.l.* within the New World tropics.

One final conclusion can be drawn from the discussion of the three genitalic characters above: the distribution of the apotypic states is consistent with the interpretation of *Siphona s.l.* as a monophyletic lineage, which is independently

supported by two synapotypies of first instars (states P32 and P33). Unfortunately the distributions of the apotypic states of these three characters are too phylogenetically equivocal to include as primary or secondary synapotypies of higher clades of *Siphona s.l.*
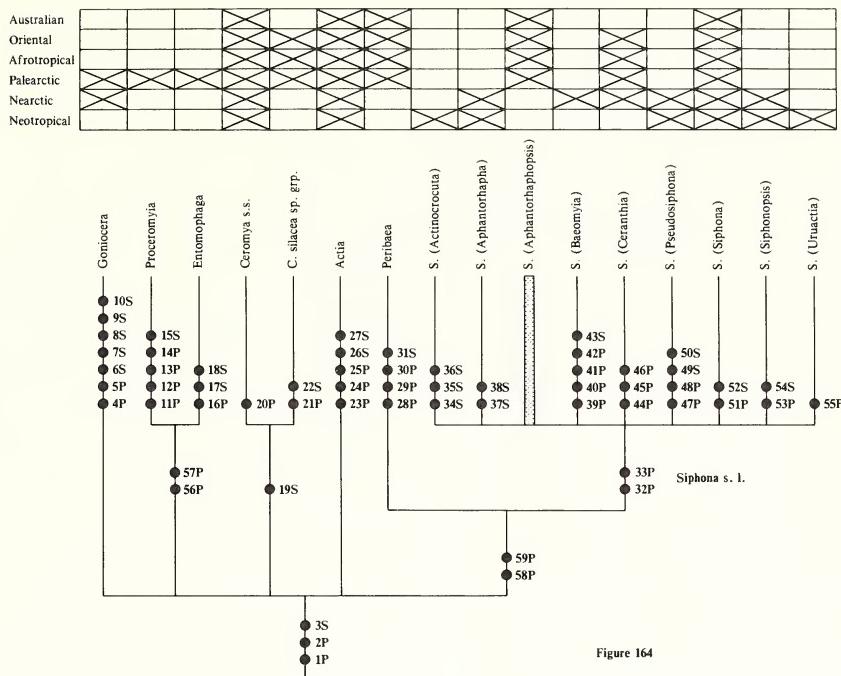
Fig. 164. Cladistic relationships and geographic distribution of the genera and subgenera of the Siphonini. Primary and secondary synapotypies are denoted by the suffixes **P** and **S** respectively. The numbered synapotypies are explained in the Evolution chapter and do not correspond to the numbers given to characters in the Structural Features chapter.
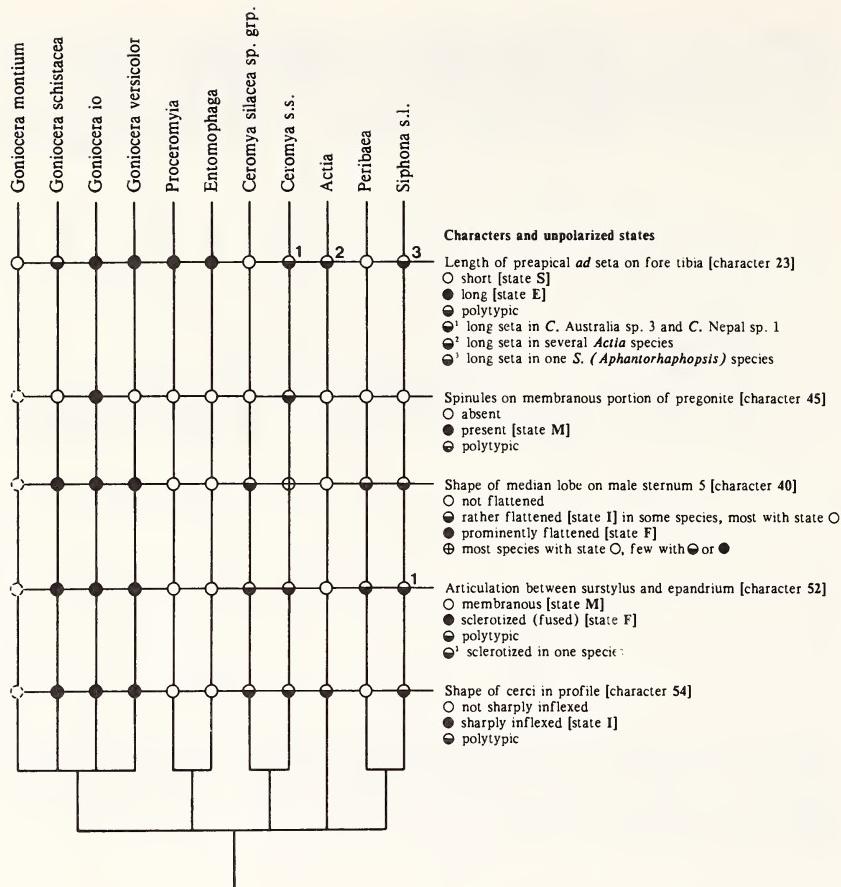
Figure 165

Fig. 165. Distribution of states for five characters relevant to the interpretation of the cladistic relationships of *Goniocera* B. & B. The male genitalia of *Goniocera montium* were not examined.
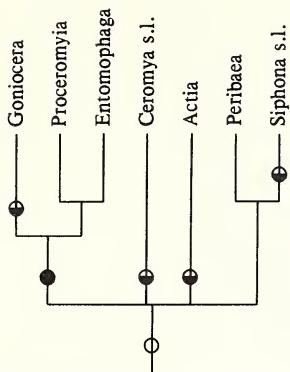
Fig. 166. Long preapical *ad* seta on fore tibia interpreted as synapotypic of *Goniocera* and the *Proceromyia-Entomophaga* lineage.
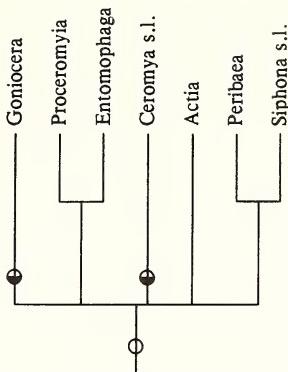
Fig. 167. Independent evolution of spinules on pregonite of *Goniocera io* and *Ceromya s.s.* (same as Fig. 210).
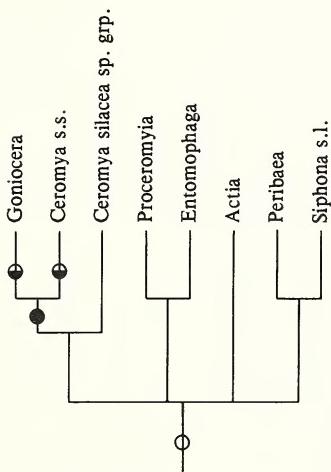
Fig. 168. Spinules on pregonite interpreted as synapotypic of *Goniocera* and *Ceromya s.s.*
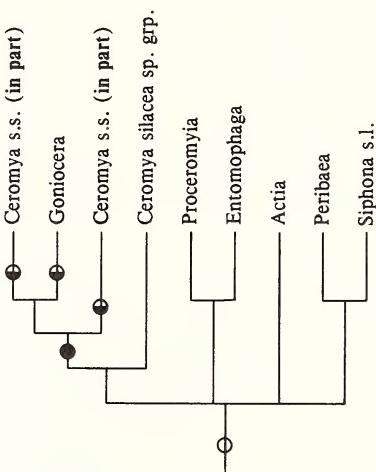
Fig. 169. Spinules on pregonite interpreted as synapotypic of *Goniocera* and *Ceromya s.s.*, with the former a derived subgroup of the latter.

Figs. 166–169. Varied interpretations of the cladistic relationships of *Goniocera* B. & B. See Fig. 165 for explanation of character states and text for discussion. Open circles indicate plesiotypic states, solid dots indicate apotypic states, and half solid dots indicate the presence of both states within a taxon: 166, cladistic relationship of *Goniocera* based on long preapical *ad* seta on fore tibia as an apotypic state; 167, cladistic relationship of *Goniocera* based on independent evolution of spinules on the male pregonite of *Goniocera io* and *Ceromya s.s.* species; 168, *Goniocera* and *Ceromya s.s.* as sister groups based on spinules on male pregonite as synapotypy; 169, *Goniocera* as derived subgroup of *Ceromya s.s.*, based on one interpretation of spinules on male pregonite as synapotypy.
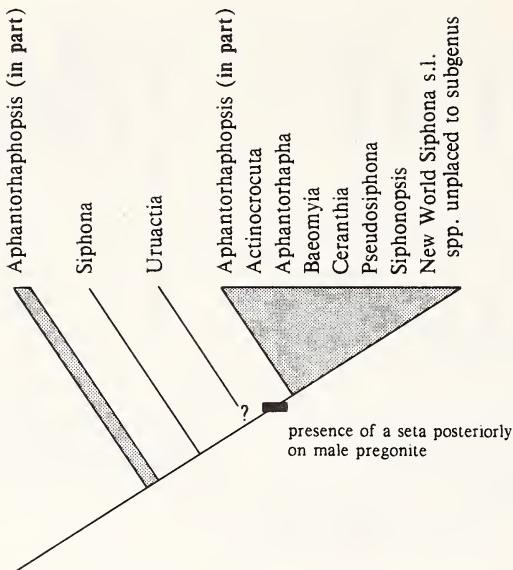
Figure 170
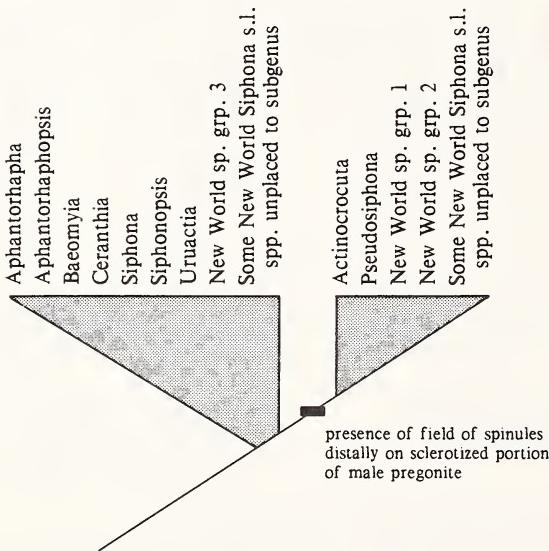
Figure 171

170, One interpretation of the cladistic relationships within *Siphona s.l.*, based on presence of a seta posteriorly on male pregonite as synapotypy. 171, One interpretation of the cladistic relationships within *Siphona s.l.*, based on presence of spinules on the sclerotized portion of male pregonite as synapotypy.

Historical zoogeography

The Siphonini are not ideal for zoogeographic analysis because they are unknown from fossils, their sister group has not been determined and their phylogenetic history is not well resolved. It is therefore necessary to take a general approach to interpreting their zoogeographic history. Accordingly, I draw very heavily upon the studies of others concerning both physical and biotic aspects of earth history to help infer a little about how siphonines came to be distributed as they are. In this section emphasis is placed on interpreting the geographic history of New World siphonines.

The geographic distribution of the major lineages of the Siphonini are detailed in the species lists and Geographic Distribution sections of the Classification chapter, and summarized by region in Fig. 164. Eight patterns of distribution are evident among these lineages:

(1) cosmopolitan — *Ceromya s.s., Actia* and *S. (Siphona)*.

(2) widespread Old World-Nearctic — *S. (Ceranthia)*.

(3) widespread Old World — *Ceromya silacea* species group, *Peribaea* and *S. (Aphantorhaphopsis)* (the latter is polyphyletic or paraphyletic with respect to other *Siphona s.l.* species, but is apparently without close affinities with New World *Siphona s.l.* species).

(4) Holarctic — *Goniocera*.

(5) Palearctic — *Proceromyia* and *Entomophaga*.

(6) Nearctic — *S. (Baeomyia)*.

(7) Nearctic-Neotropical — *S. (Aphantorhapha), S. (Pseudosiphona), S. (Siphonopsis)* and New World *Siphona* species groups 2 and 3.

(8) Neotropical — *S. (Actinocrocuta), S. (Uruactia)* and New World *Siphona* species group 1.

Absent from the above patterns is any taxon of widely, and strictly, Southern Hemisphere distribution. Similarly, no such pattern is evident among species groups of the three cosmopolitan taxa. This negative evidence suggests that the Siphonini did not diversify in the Southern Hemisphere until after the breakup of Gondwanaland, either because they were initially of Laurasian distribution or they evolved somewhere in the Southern Hemisphere after South America, Africa and Australia drifted apart.

Breakup of Gondwanaland began with the separation and northward movements of Africa and India from the other southern continents, followed by separation of South America and then Australia from Antarctica. Timing of each of these events is inexactly known, though most workers agree that South America and Africa were in close proximity until the Late Cretaceous, and South America and Australia were narrowly jointed *via* Antarctica (or only narrowly separated) into the Early Tertiary (Adams 1981, Smith *et al.* 1981). Not only is the geologic timing of these events important to the zoogeographer, but also are the varied dispersal abilities of different organisms and the changing environmental conditions of the Cenozoic. All of these

factors affected the probability of particular organisms reaching new habitations.

Siphonines are moderately good dispersers, as judged from their limited species numbers on Madagascar and islands of the Caribbean and southeast Asia, and their virtual absence from mid-oceanic islands. This ability to cross moderate water gaps implies that siphonines cross barriers more readily than most terrestrial vertebrates, and can doubtfully cross such large distances as those now between South America, Africa and Australia.

I infer from the lack of a Gondwanaland distribution pattern among siphonines, the timing of the breakup of Gondwanaland and the dispersal powers of siphonines, that the history of the Siphonini in the Southern Hemisphere is entirely Cenozoic in age. This age could be extended to the Late Cretaceous if southern continents were farther apart at the beginning of the Cenozoic (or siphonines poorer dispersers) than here suggested.

I noted above that siphonines might have originated in Laurasia prior to the breakup of Gondwanaland (*i.e.* during the Cretaceous). This possibility cannot be corroborated or rejected by an analysis of siphonine relationships and present day distributions (Fig. 164). Instead, such an early age for the Siphonini is considered highly unlikely because fossil Calyptratae are virtually unknown from pre-Tertiary deposits, and extant calyptrates show few and suspect Gondwanian distributions (O'Hara 1983a: 329).

In summary, no evidence supports a pre-Tertiary origin of the Siphonini. Therefore, in the ensuing discussion, all aspects of the zoogeographic history of the Siphonini are couched in terms of Cenozoic events.

Large and small scale Cenozoic changes in earth climate, sea level, biotic associations and position and topography of continents must have produced a shifting array of physical and ecological barriers to the dispersal of siphonines. The interpretation of siphonine distribution patterns is inferred from a comparison of siphonine distribution (and hypothesized relationships) with major changes in earth history. As an introduction to the analyses of siphonine distributions, some of the major physical and ecological changes that are thought to have occurred during the Cenozoic are outlined. Most of this account is summarized from Adams (1981), with additions as noted.

Europe and Asia became separated by the Turgai Strait during Early Tertiary time, while the Tethys Sea slowly narrowed as Africa and India drifted northward. South America, severed from Africa in the Cretaceous and from Antarctica in the Late Paleogene, remained isolated from other land masses until the Pliocene. North America was in land contact with both Europe and Asia in the Early Tertiary. Two or three land bridges spanned the North Atlantic during the Paleogene, providing good avenues for biotic exchange between North America and Europe during most of this period. Though the histories of these land bridges are geologically complex and difficult to interpret, remnants of a North Atlantic corridor might have persisted even into the Miocene (Matthews 1979, Eldholm and Thiede 1980, McKenna 1983).

However, scanty fossil evidence of a functional Miocene corridor implies that it was, at best, a weak filter bridge at that time (also, Beringian interchange at that time could have produced similar fossil distributions).

Beringia probably provided a land corridor between Asia and North America throughout most of the Cenozoic until periodically submerged during the Quaternary (McKenna 1983). However, Beringia occupied a more northerly position with respect to the earth's rotational pole during the Early Tertiary, so probably experienced a more extreme climate at that time than its North Atlantic counterpart. Hence, Beringia might have functioned more as a filter bridge than a land bridge in the Early Tertiary before assuming a relatively more southern position (McKenna 1983).

The climate during the Paleogene was considerably warmer than now even at high latitudes, peaking during the Early Eocene after several warm-cool fluctuations (Wolfe 1978, 1980, Axelrod 1983, Romero 1986). By Middle Eocene the earth's climate had begun to deteriorate, causing retreat of paratropical forests (*sensu* Wolfe 1978) from high latitudes and their replacement with more temperate adapted elements. By the end of the Paleogene a seaway opened between Antarctica and Australia, and the Turgai Straits closed between Europe and Asia.

Climatic cooling continued, with periodic fluctuations, in the Neogene. Faunal exchange increased between Africa and Eurasia as the Tethys Sea narrowed, though changes in sea level alternately facilitated and hindered such exchange, as it did also as the Australian plate converged upon the island archipelago of southeast Asia (Martin 1982). Large scale climatic and biotic changes took place as the Tethys Sea closed and major mountain building occurred, particularly between Asia and the Indian subcontinent and along the western edge of the Americas. Antarctica grew progressively colder, with development of a polar ice cap in the Late Miocene (Mercer and Sutter 1982). Marked increase in exchange between North and South America began in the Pliocene with the emergence of a land corridor between these continents, which has persisted under changing ecological regimes to the present day. Most dramatic of all were the wide scale changes to the earth's climate and biota during the ice ages of the Pleistocene.

The following discussion about the zoogeographic history of the Siphonini is partly based on three important assumptions: (1) siphonine evolution and diversification took place under the general Cenozoic conditions just described, (2) siphonines were more likely to shift geographically than ecologically in the face of changing climatic conditions (in the same way as most species are thought to have responded to Pleistocene climatic changes, for example), and (3) general patterns of siphonine distribution have not been profoundly limited by host availability (one might expect that siphonines, as parasitoids, have been constrained in their ability to diversify in newly invaded regions by lack of suitable hosts, yet no such constraints appear to have affected siphonine distributions).

Two patterns of distribution are recognized among strictly Old World siphonines - one Palearctic and the other widespread (see list of patterns at beginning of section). The Palearctic pattern is shared by sister genera *Proceromyia* (with two eastern species) and *Entomophaga* (with two western species). A past vicariance of a widespread ancestor into an eastern *Proceromyia* and western *Entomophaga* lineage is the most obvious explanation for this pattern. However, these lineages may be relatively basal to siphonine phylogeny, so might once have been more diverse (and possibly more widespread) than at present. This might also account for the marked external differences among the extant species. On the other hand, the restriction of extant species to the Palearctic region, and a temperate environment, is suggestive of a more recent origin (perhaps during the Miocene when temperate forests reached their maximum extent; Graham 1972, Axelrod 1983).

Belonging to the second Old World distribution pattern are *Peribaea*, the *Ceromya silacea* species group and *S. (Aphantorhaphopsis)*. *Peribaea* is widespread throughout all Old World regions, with more described species in the Australian region than any other siphonine lineage (partly, but not entirely, a reflection of recent taxonomic work by Shima 1970a). *Peribaea* species are also recorded from such islands as Fiji, Seychelles, Mauritius and Madagascar, so it is paradoxical that this highly vagile and speciose group has not reached the New World.

Little can be written about the distributions of the *Ceromya silacea* species group and *S. (Aphantorhaphopsis)* except that they, like other widespread taxa except *Peribaea*, have depauperate faunas in the Australian region. This pattern undoubtedly reflects the isolation of Australia, New Guinea and associated islands from Asia during most of the Cenozoic.

Two distribution patterns, those of *Goniocera* and *S. (Ceranthia)*, have Nearctic-Old World elements. The former is known from four temperate species, one in eastern North America and three in Europe. The phylogenetic relationships among these species are unknown, though the presence of possible sister groups to *Goniocera* in the Old World suggests that the genus arose there. Later dispersal to, and differentiation in, the New World probably occurred when temperate forests were widespread at high latitudes and continuous between North America and Eurasia. Such conditions developed during the Early Neogene, presumably after severance of a functional North Atlantic land bridge (though Axelrod (1983) hypothesizes exchange of temperate forest elements across both Beringia and a North Atlantic corridor in the Miocene). Therefore, barring long range dispersal from Europe, entry to the New World was probably through Beringia. The restricted ranges of the extant species, all far removed from Beringia yet cool adapted, are best accounted for by either an Early Neogene vicariance of a Holarctic species (with changes in range due to Miocene mountain building and global climatic changes), or a more recent vicariance followed by Pleistocene displacements (Fig. 172).

The subgenus *S. (Ceranthia)* also has a Nearctic-Old World distribution pattern. Old World species of this subgenus are almost equally split in number between the

Palearctic and Afrotropical regions, while the Nearctic element is strictly temperate. As with *Goniocera*, the temperate element of *S. (Ceranthia)* in the Nearctic region probably resulted from dispersal from the Old World during the Neogene (Fig. 172), possibly during the Miocene judging from the moderate number of Nearctic species (mostly undescribed).

Among the remaining distribution patterns are four *Siphona* lineages only recorded from either the Nearctic (*S. (Baeomyia)*) or Neotropical (*S. (Actinocrocuta)*, *S. (Uruactia)* and New World *Siphona* species group 1) region. In patterns such as these where all members of a lineage are within one region, it is most parsimonious to postulate that each lineage evolved from an ancestral species in that region. This is almost certainly true of the three Neotropical lineages, since *S. (Uruactia)* is only known from two species in Peru and Ecuador, and *S. (Actinocrocuta)* and N.W. *Siphona* sp. grp. 1 are members of a monophyletic group (Fig. 171) of almost entirely Neotropical distribution. The history of Neotropical siphonines is discussed in more detail further on.

Three siphonine lineages have cosmopolitan distributions: *Ceromya s.s.*, *Actia* and *S. (Siphona)*. The zoogeographic history of *S. (Siphona)*, with special emphasis on the North American fauna, was treated elsewhere (O'Hara 1983a). I hypothesized that periodic exchange between the Old and New World took place among *S. (Siphona)* species groups from the Eocene to the Pleistocene. In general, Holarctic elements were hypothesized as Middle Tertiary to Quaternary in age (Fig. 172) and more tropically distributed taxa with Old World-New World affinities of older ancestry (Fig. 173). I predict that similar hypotheses can explain the distributions of *Ceromya s.s.* and *Actia* species groups when these are phylogenetically analyzed.

It would appear from lists of described species that cosmopolitan lineages of the Siphonini are low in species diversity in both the Neotropical and Australian regions. Though this is so for the Australian region, it is not for the Neotropical region. The pattern of low diversity in the Australian region is the same as for most Old World siphonine lineages with Australian members, reflecting the relative isolation of that region from Asia for most of the Cenozoic (see above). South America was also isolated from other continents for most of the Cenozoic, so the high diversity of siphonines in that region poses an especially interesting zoogeographic problem.

The Neotropical region has three endemic siphonine taxa (*S. (Actinocrocuta)*, *S. (Uruactia)* and New World *Siphona* species group 1), five lineages shared only with the Nearctic region (*S. (Aphantorhapha)*, *S. (Pseudosiphona)*, *S. (Siphonopsis)* and New World *Siphona* species groups 2 and 3), and elements of three cosmopolitan groups (*Ceromya s.s.*, *Actia* and *S. (Siphona)*). How can this high diversity of Neotropical siphonines be explained? Whether the ancestors of most Neotropical lineages originated in that region or in the Old World is of minor importance, as the major pathways of movement (*i.e.* between the Americas and between North

America and Eurasia) would be the same even if the direction were reversed. The phylogenetic relationships are presently too inadequately known in *Ceromya s.s.*, *Actia* or *S. (Siphona)* to strongly argue for or against an Old World origin of each (*cf.* O'Hara 1983a, in which an Old World origin was favored partly because the high diversity of these taxa in the Neotropical region was unknown). However, the possibly basal lineages of the Siphonini are Old World in distribution, so for the purpose of this discussion an Old World origin will be assumed for these three taxa. Certain lineages of *Siphona s.l.* are certainly New World in origin, as the distributions in Fig. 164 and possible relationships in Fig. 171 illustrate.

It follows from the review above about Cenozoic events and general assumptions about siphonine evolution, that the only route to (or from) South America during the Cenozoic would have been through North America. It is well known on the basis of both geologic and fossil evidence that South America was physically isolated from other continents during most of the Cenozoic. However, there were two periods of faunal and floral exchange with North America. The first is hypothesized as Paleocene (and Late Cretaceous), as evidenced and/or postulated from geologic evidence (Coney 1982) and distributions of angiosperms (Gentry 1982), herpetofauna (Savage 1982, Estes and Báez 1985), atherinid fishes (White 1985), colubrid snakes (Cadle 1985) and mammals (Gingerich 1985, Webb 1985a). The exact nature of the Paleocene connection is uncertain, though there is general agreement that it was probably an island chain and functioned as a filter bridge. Certain organisms evidently crossed this bridge more readily than others. The suggestion that this filter bridge persisted into the Eocene is not well documented.

The second period of biotic exchange between the Americas is very well corroborated and the subject of a recent multi-authored book, "The great American biotic interchange" (Stehli and Webb 1985). This interchange began in the Pliocene (about 3mybp [million years before present] according to most sources, but 5mybp according to others) with the emergence of a complete land corridor between the Americas. This corridor has alternately functioned, from that time to the present, as a route of dispersal for certain organisms and a barrier to others, as global climate fluctuated throughout the ice ages of the Pleistocene.

It is extremely doubtful that the diversity of Neotropical Siphonini can be entirely accounted for by immigrations since the Pliocene, though it is clear that present day siphonine sister species and sister groups distributed between Middle and South America are evidence of siphonine participation in the "great biotic interchange". The important question to be addressed here is whether earlier siphonine arrivals to South America were over a water gap or across a filter or land bridge.

Assuming (as above) that siphonines originated in the Old World during the Cenozoic and have generally maintained their ecological affinities during periods of major climatic change, it follows that ancestors of extant Neotropical siphonines entered North America from Eurasia at a time during the Tertiary when land bridges

between the continents were subtropical to tropical in nature. As the only such land bridges were at high latitudes (Beringia and across the North Atlantic), and the climatic optimum of the Early Eocene was the only time during the Tertiary that these corridors supported such conditions, it is hypothesized that an ancestral stock of Neotropical Siphonini entered the New World at that time. (Webb, comparing mammal faunas of Europe and North America, called the warm period of the Early Eocene "the most intensive intercontinental interchange between any two continental mammal faunas before the Great American Interchange." (1985a: 207)) Then, as global climate cooled in the latter part of the Paleogene and temperate forests began to replace the retreating tropical forests, siphonines became increasingly more southerly distributed in North America (Fig. 173). This sequence of events was proposed to explain Mexican elements of *S. (Siphona)* (O'Hara 1983a), and to explain some elements of the Central American herpetofauna (Savage 1982).

The zoogeographic scenario has thus far tended toward a vicariant explanation of siphonine history. However, only dispersal events over a wide water gap or across a weak filter bridge can account for the earliest siphonine entries into South America (Fig 173). Even if siphonines colonized North America in the Eocene and reached the southern part of the continent shortly thereafter, they would still have arrived too late to cross the Paleocene filter bridge into South America. There is no evidence from the Eocene to the Miocene of a land corridor between the Americas, and little evidence for an even weak filter bridge until the Late Miocene. (An intermittent filter bridge is mostly hypothesized to explain the first appearance of certain organisms in the fossil record of either North or South America - *e.g.* Stehli and Webb 1985, Chapter 1.) Whether or not a filter bridge existed from time to time during this interval, there is nevertheless a suggestion of faunal and floral exchange, as inferred from cricetine rodents (Hershkovitz 1966, 1972), angiosperms (Raven and Axelrod 1975), carabid beetles (Ball 1978, Allen and Ball 1980, Ball and Shpeley 1983, Noonan 1985), mammals (Webb 1985b), ectoparasites of mammals (Wenzel and Tipton 1966), primates and caviomorph rodents (Wood 1985 [though the zoogeographic interpretations of these groups are highly controversial]) and herpetofauna (Vanzolini and Heyer 1985). Siphonines, like these taxa, seem to have preceded, as well as participated in, the "great biotic interchange" in their colonization of South America. When, and how often, is uncertain. The large clade of Neotropical *Siphona s.l.* species (Fig. 171) suggests at least a moderate history in South America (Oligocene or Miocene?). The high species diversity of *Ceromya s.s.*, *Actia* and *S. (Siphona)* in the Neotropics also suggests that members of these lineages reached South America before formation of the Pliocene land bridge (Fig. 173).

A minor element of the Nearctic siphonine fauna is possibly derived from tropical adapted siphonines. Two sources are hypothesized: Firstly, differentiation of temperate adapted taxa from tropical adapted taxa as subtropical to tropical

conditions over most of the region were replaced by warm temperate to boreal conditions after the climatic deterioration of the Eocene. (Similar to the hypothesis that the vegetation of the Sonoran Desert is mostly derived from contiguous, less arid adapted, taxa; Axelrod 1979.) It has been assumed throughout this section that the evolution of new ecological affinities such as this have played a minor role in the history of New World Siphonini - an analysis of relationships among North American *S. (Siphona)* suggests this is a valid assumption (O'Hara 1983a). Secondly, a few Nearctic taxa are likely derived from reinvasion of the region from Middle or South America (Fig. 172). Most of these taxa are southerly distributed in the Nearctic region.

Perhaps as more organisms are studied, particularly vagile organisms like many insects, vicariance biogeographers will recognize biotic exchange between North and South America as a zoogeographic problem demanding of both dispersal and vicariant explanations. Cracraft (1975), for instance, considered the patterns of distribution between the Americas as inadequately interpretable by vicariant events alone. It must be realized that in certain areas dispersal cannot be ignored in favor of the "rigorous" method of vicariance biogeography. Erwin, discussing how vicariance biogeographers interpret distributional data, wrote:

> "The major flaw of the entire Croizat school [vicariance biogeography] is that their method is no more "general" [meaning "vicariance ... is to be assumed and dispersal only explains special cases"] than that of the dispersal or centrist's school, because biological organisms are not generalists! All groups and subsets of groups have their own unique powers of movement or lack of movement and each group must be dealt with on its own merits with full knowledge of powers of dispersal, passive or active, or lack thereof." (1979: 357)

Summary of the zoogeographic history of the Siphonini

(1) The Siphonini are hypothesized as originating during the Cenozoic, because of the virtual absence of Mesozoic fossil Calyptratae and lack of recognizable Gondwanian distributions among extant siphonines.

(2) The present distributions of sister genera *Proceromyia* and *Entomophaga* in eastern and western Palearctic, respectively, suggest a past vicariance of a widespread Palearctic ancestor. However, the possibly rather basal position of this clade in the Siphonini might reflect an older ancestry than otherwise suspected.

(3) A general pattern of low diversity is noted in the Australian region for most siphonine lineages. This pattern is explained by the relative isolation of Australia and associated islands from southeast Asia during most of the Tertiary, which prevented rapid dispersal of siphonines into the region, and

hence limited the opportunity for speciation therein.

(4) It is assumed from largely inferential evidence that the Siphonini originated in the Old World, so the high diversity of New World siphonines must be explained by northern routes of entry (across Beringia and the North Atlantic) from Eurasia (Figs. 172-173).

(5) Most Nearctic siphonines are descendants of Old World taxa that became widespread in the Holarctic region since the Middle Tertiary, as temperate and boreal conditions replaced the more tropical conditions of the Eocene (Fig. 172). A minor component of the Nearctic fauna is derived from tropical adapted siphonines. These either differentiated *in situ* from tropical adapted siphonines as global climate cooled and temperate forests expanded, or reinvaded the Nearctic region from Middle or South America (Fig. 172).

(6) It is assumed that siphonines have generally maintained their ecological affinities through periods of climatic change. Therefore, Neotropical siphonines are hypothesized as descendants of Old World, tropical adapted, siphonines that became widespread in the Holarctic region during the climatic optimum of the Eocene. Subsequent deterioration in climate and periodic crossing of a water barrier (weak filter bridge?) between the Americas during the Middle to Late Tertiary, and speciation in South America, accounts for the high diversity of some siphonine lineages in the Neotropical region (particularly the large clade of Neotropical *Siphona s.l.* species) (Fig. 173).

(7) Sister species and groups distributed on either side of the Isthmus of Panama (mostly Middle America-South America) are evidence of siphonine participation in the "great American interchange" of the Pliocene and Quaternary.

Predictions and tests of zoogeographic hypotheses

(1) No Gondwanian distribution patterns will be recognized among siphonines.

(2) More resolved phylogenies of both higher taxa and species groups of the Siphonini will more firmly establish the Old World origin of most lineages and corroborate the suspected affinities between Nearctic and Palearctic Siphonini (*i.e.* similar relationships are expected to those hypothesized for *S. (Siphona)*; O'Hara 1983a).

(3) The largely endemic nature of Neotropical Siphonini will become apparent as relationships to faunas of other regions are resolved, reflecting the old origin of the fauna from Early Eocene, North American, ancestors.

(4) Indirect corroboration will be forthcoming from similar interpretations of Neotropical elements of similarly distributed taxa, and corroboration or refutation of aspects of earth history herein reviewed.
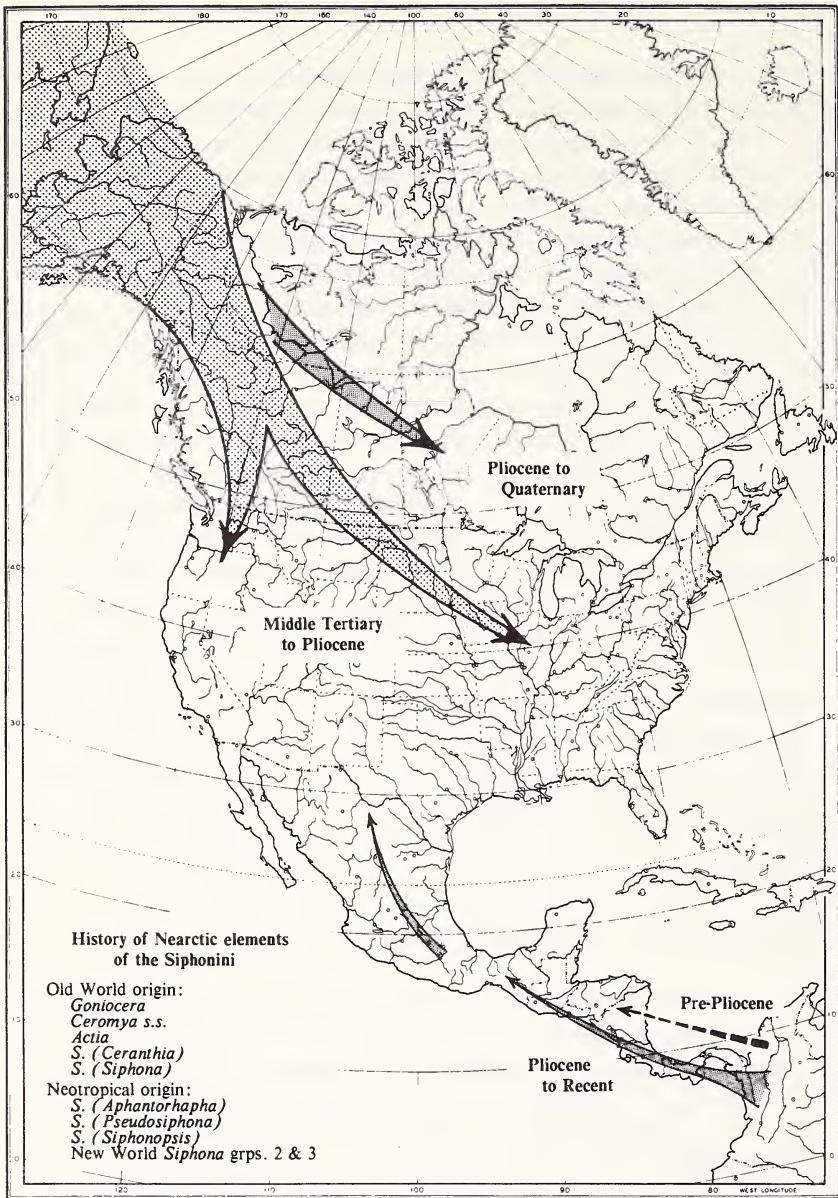
Fig. 172. General zoogeographic history of Nearctic elements of the Siphonini. Three ancestral sources are hypothesized as contributing to the siphonine fauna of the Nearctic region:

(1) most taxa are derived from Old World ancestors crossing Beringia from the Middle Tertiary to the Pleistocene. These taxa evolved in association with warm temperate to boreal biomes.

(2) a minor component is derived from *in situ* differentiation, as tropical adapted siphonines shifted southward, and temperate forests expanded, following the climatic deterioration of the Eocene.

(3) another minor component, mostly southern Nearctic in distribution, are taxa that reached the Nearctic region from Middle or South America. Taxa reaching North America from South America did so either before (very few taxa) or after a land corridor was established between these continents in the Pliocene.

Eocene paratropical forest

Middle Tertiary southward shift

Middle and Late Tertiary over-water dispersal

Pre-Pliocene history of Neotropical elements of the Siphonini

Actia
Ceromya s.s.
S. (Actinocrocuta)
S. (Aphantorhapha)
S. (Pseudosiphona)
S. (Siphona)
S. (Siphonopsis)
S. (Uruactia)
New World *Siphona* sp. grp. 1
New World *Siphona* sp. grp. 2
New World *Siphona* sp. grp. 3
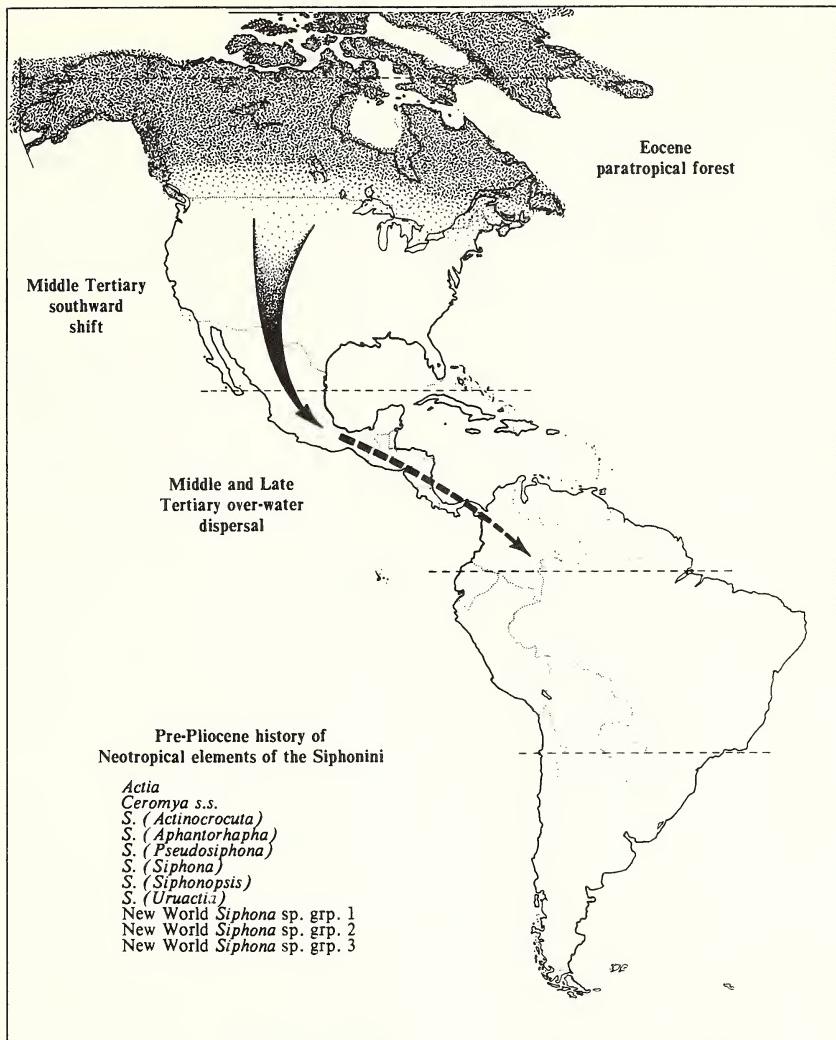
Fig. 173. Pre-Pliocene zoogeographic history of Neotropical Siphonini. An ancestral stock of tropical adapted siphonines are hypothesized to have reached North America across Beringia and/or North Atlantic land bridges during the climatic optimum of the Early Eocene. These taxa became more southerly distributed as global climate deteriorated. In the absence of a land bridge between the Americas for most of the Cenozoic, ancestral siphonines of several major lineages crossed a water gap (weak filter bridge?) to reach South America. Exchange was facilitated between the Americas after establishment of a land corridor in the Pliocene (as siphonines participated in the "great American interchange").

CONCLUDING REMARKS

I have set forth in this paper a revised classification of the supraspecific taxa of the Siphonini. For the first time, the markedly different classifications of the Old and New World Siphonini have been meshed. Relatively few taxonomic changes are proposed as a result of this action, except for a number of changes in rank to update and balance the classification (particularly with respect to genus group names among New World *Siphona* group taxa) and several new higher level combinations required on phylogenetic grounds.

Considerable effort was made to classify - and provide a key for identification of - Neotropical siphonines, even though most of the known species are undescribed. However, this effort is but a preliminary attempt, and apt to be inadequate for some taxa. Present categories will need to be modified, and new subgenera of *Siphona s.l.* will almost certainly need to be erected, when the diverse siphonine fauna of the Neotropical region is more completely studied and the species described.

ACKNOWLEDGEMENTS

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POSTSCRIPT

Several papers dealing with siphonines have recently been published while this paper was in press. These are listed below.

O'Hara, J.E. 1988. Survey of first instars of the Siphonini (Diptera: Tachinidae). Entomologica scandinavica **18**: 367-382. This paper is cited as "In press 'a'" in the text and references above.

O'Hara, J.E. 1988. Correlation between wing size and position of a hind crossvein in the Siphonini (Diptera: Tachinidae). Journal of Natural History **22**: 1141-1146. This paper is cited as "In press 'b'" in the text and references above.

Herting, B. 1987. Beiträge zur Kenntnis der paläarktischen Raupenfliegen (Dipt. Tachinidae), XVII. Stuttgarter Beiträge zur Naturkunde (A) **408**: 1-14. A new siphonine species, *Ceranthia impropria* Herting, is described in this work. Dr. Herting kindly allowed me to examine the only known specimen of that species when I visited him in 1985. I provisionally follow Herting's placement of the species in *Ceranthia* (*i.e. Siphona* (*Ceranthia*) in my classification); however, I need to examine a male specimen (particularly the male genitalia) before placing the species with confidence.

Cantrell, B.K. 1988. The comparative morphology of the male and female postabdomen of the Australian Tachinidae (Diptera), with descriptions of some first-instar larvae and pupae. Invertebrate Taxonomy **2**: 81-221. First instars and the male and female genitalia of some Australian siphonines are described and illustrated.

I discuss in the text a nomenclatural problem involving the name *Peribaea orbata*

(see *Peribaea* Section). The matter is thoroughly reviewed by R.W. Crosskey and H. Shima (1988) in a case before the International Commission on Zoological Nomenclature: Case 2632. *Tachina orbata* Wiedemann, 1830 (currently *Peribaea orbata*; Insecta, Diptera) : proposed confirmation of neotype designation. Bulletin of Zoological Nomenclature **45**: 199-201.

INDEX TO NAMES OF TAXA
(Synonyms in italics)

COMMENTARY

[Commentary is a section of *Quaest. Ent.* that appears from time to time, and will contain expressions of opinions about general items, controversial or otherwise, that ought to be of interest to many of our readers. These contributions will not be refereed because they are intended to be free expressions of opinion. Changes by the Editor might be made to the form of presentation, but not to its substance. Remarks that are deliberately abusive or insulting will not be published. Rebuttals to previously expressed views will be considered, but the journal is under no obligation to publish them.

The Editor]

Following is an extended book review. Because of the potentially controversial nature of some of the comments, it seems more appropriate to place the review in a section of the journal that invites dialogue--hence its location in "Commentary".

LIEBHERR, J. K. (Editor). 1988. Zoogeography of Caribbean Insects. Comstock Publishing Associates, Cornell University Press, Ithaca and London. xi + 285 pp. Price, $39.95 (U.S.)

Printed on acid-free paper, this volume is attractively hardbound, with dark green covers. On the front cover is a figure illustrating the geographical distribution and reconstructed phylogeny of the drosophilid genus group *Pseudiastata* and an adult of the West Indian *Mayagueza argentifera,* a member of this taxon. It is an excellent illustration and provides a focus on the subject matter of the book. The lighter green end-papers inside the covers contain a useful map of the Caribbean Basin, including the islands of the West Indies and adjacent portions of the North, Middle, and South American mainland, complete with scale and indications of longitude and latitude.

The volume includes a preface, list of contributors, and 11 chapters. Subject and taxonomic indices end the volume. Chapter 1 is a general discussion of Caribbean zoogeography. Chapter 2 treats geological aspects; and Chapter 11 is a critique of biogeographical methods in general, and of work of the other authors of this volume, in particular.

Chapters 3 to 10 contain analyses of taxa, as follows: Lygaeidae, by J.A. Slater; auchenorrhynchous Homoptera of the Greater Antilles, by J.A. Ramos; scaritine Carabidae, by S.W. Nichols; platynine Carabidae, by J.K. Liebherr; polycentropodid caddisflies, by S.A. Hamilton; relict Drosophilidae, by D.A. Grimaldi; ants, by E.O. Wilson; and halictid bees, by G.C. Eickwort. Each taxon-based chapter is a rich source of clearly presented information, containing extensive lists of included taxa and their distributions. Most of the chapters contain very well executed illustrations of the insect group treated, or of their work, and maps and diagrams are also provided that amplify the text. The chapter by Ramos is not illustrated, and overall seems rather perfunctory.

As a carabid specialist, I was impressed especially with the execution of the distribution maps in Nichols' chapter: each with a photograph illustrating habitus of one or more species whose range is indicated by dots, etc. Much care went into the preparation of these figures, and collectively they are a valuable source of data.

Recurrent themes in the text are: occurrence of old relicts on Puerto Rico (noted by Slater, Nichols, Liebherr, and Grimaldi): and incomplete knowledge of the biota, because of insufficient collecting by appropriate specialists.

The analyses of various taxonomic groups are inconsistent in delimitation of the study area. In his concept of the West Indian Biogeographic Region, Nichols includes the Greater and Lesser Antilles, the Bahamas, Barbados (as a separate entity), South Florida, and the Yucatan Peninsula of Mexico. Wilson does not include the mainland in his treatment of the ants, but does include Trinidad and Tobago. This inclusion increases the size of the ant fauna of the West Indies by about a third. The other authors confine their study areas to the Bahamas, and Greater and Lesser Antilles, with Barbados included in the last-named island group. Such differences in definition of study area must be taken into account by those who might wish to compare taxonomic diversity of the various taxa in the West Indies.

The Editor claims in the title of the Introduction (Chapter 1) that the Caribbean area is a "fertile ground for zoogeography". He provides a clear, even-handed discussion of the history of ideas about assembly of the West Indian biota; first, postulation of land bridges to make possible movement of the ancestral terrestrial biota from mainland to islands; second, carefully reasoned dispersal theory, without invocation of land bridges; and third, plate tectonic theory, with its pieces of land, originally close to mainland Central and South America, that drifted eastward, and brought an essentially mainland biota to the development of the present Greater Antilles.

Liebherr indicates that this basic question of the mechanism of faunal assembly has not been settled, and maintains (p. 10) that "geologic data often cannot provide unequivocal answers about the history of areas, making biological data of utmost importance in the interpretation of faunal histories". He advocates use of vicariance biogeography in this endeavour. However, I doubt that conclusions drawn from biological data can be more compelling than geological data, by whatever means the former are interpreted.

The Editor makes a convincing case that the Caribbean area is fertile ground for zoogeographers. He concludes his opening chapter by indicating the great potential of data derived from insects, as follows:

1. Insects are apt to help clarify old patterns of faunal relationships, because the West Indies have a fair number of taxa that exhibit relations with Africa rather than with New World taxa, and this implies Gondwanian connections. Liebherr implies that such relationships are direct, *i.e.,* without extinct New World mainland intermediates, or even

intermediates that have yet to be discovered.

2.   Many taxa in the Antilles are conspecific with or very closely related to mainland Neotropical species. These taxa indicate overwater dispersal between mainland and islands.

3.   There is a rich endemic fauna in the islands, which provides an "extensive potential data base for intra-island analyses".

He notes, however, that the insect fauna of the Antilles is not well known, and that much field work is required to elucidate "species distributions and habitat requirements". Mindful of the destruction of habitats that is taking place in the islands and the effect that such will have on distribution patterns before there is the chance to study them, he advocates activity in protection of the biota.

Thomas W. Donnelly, a geologist and dragon fly specialist with extensive experience in the Caribbean area, and thus sympathetic to the requirements of biogeographers in interpreting geological history, provides important background information in his chapter entitled "Geologic Constraints on Caribbean Biogeography". Reviewing the evidence on the basis of plate tectonic theory, Donnelly argues that an island arc formed between Central and South America, providing a tenuous connection between these land masses. In latest Cretaceous and early Cenozoic times, this arc was broken into fragments as a "flood basalt moved eastward" (p.33). These fragments, or terranes, formed the present Greater Antilles, but some (such as proto-Jamaica) were totally submerged for extended periods. Cuba was formed in the late Cretaceous by diverse terranes that were "swept northward" with the opening of the Yucatan Basin. In the Middle Cenozoic (Oligocene to early Miocene), the continued eastward movement of the Caribbean Plate closed the gap that separated Central and South America and another island arc system served as a limited filter bridge for terrestrial organisms, between the two continents. The lesser Antilles, during mid-Cenozoic, was a series of separate fragments more distant from South American than from the Greater Antilles. The volcanic arc that formed during the late Cenozoic provided a filter bridge for dispersal from South America, but geological evidence minimizes the probability of an earlier Cenozoic connection of the mainland and the Lesser Antillean arc.

For most of late Mesozoic and Cenozoic time, faunal movements into the proto-Antilles and Greater Antilles would have required overwater dispersals in the order of tens of kilometers. For brief periods, the water gaps might have been "relatively narrow", and there could have been terrestrial connections with northern Central America, and between the islands. Overwater dispersal must be emphasized, though geologists are beginning to find evidence for "limited vicariant interchange".

Donnelly emphasizes that changing climatic conditions during the Cenozoic must have had profound influence on distribution of the biota. Using evidence of lateritic soils in the Greater Antilles, he postulates less moderate climates during the middle Cenozoic than at present, with markedly alternating wet and dry periods. The

development of the Central American isthmus during the Pliocene must have led to profound climatic change, and during the Pleistocene there is strong evidence for aridity during the glacial maxima.

The main point of all this is that biogeographers must be very cautious about invoking interruptions of continuous land connections to explain present-day vicariant distributions of related taxa.

One might think that Donnelly's paper would have caused all of the other symposiasts to emphasize dispersal theory in explaining extant distribution patterns. In fact, this did not happen, with the resulting biogeographic analyses forming two groups: those postulating dispersal theory as the principal means of explaining extant distribution patterns; and those postulating elimination of former land connections and subsequent establishment of new connections as the basis for vicariant patterns.

Of course, vicariant distribution patterns result, whatever mechanism gives rise to geographically isolated descendants of an originally continuously distributed ancestral stock. Consequently, it is incorrect to use "vicarism" as a term for a process. However, for want of a better term, I will use vicarism as is accepted by some biogeographers to designate postulation of interruptions of continuous parental ranges as the normal cause of subsequent vicariant distribution patterns of descendants.

Authors adopting dispersal as the principal cause of vicariant distributions in the Caribbean area are Slater, Nichols, Wilson, and Eickwort. Vicarists are Liebherr, Hamilton, and Grimaldi. Wilson hardly acknowledges the existence of the vicarist school, and interprets the Antillean ant fauna mainly in terms of island biogeographic theory.

An interesting age correlation emerges. Of the dispersalists, three (Slater, Wilson, and Eickwort) are appreciably older than the vicarists. Nichols is the exception. As the youngest and least experienced of the symposiasts, perhaps he was the most inclined to pay attention to Donnelly. The older individuals had their ideas formed before the heyday of the vicarists, whereas the others have been developing their careers during the vicarism period, and thus perhaps they were influenced by recent events, not to mention forceful protagonists.

Slater argues that congruence of distribution patterns of different groups may not be applicable in establishing vicariance explanations to islands located relatively close to different source areas. Taking exception to the late D.E. Rosen's expressed antipathy to using dispersal to explain biotic complexity, Slater (p.39) notes that "if wind patterns, ocean currents, similarity of habitats, and relative proximity of areas persist over a reasonable period of time, congruent patterns could be developed by dispersal as well as by vicariance". He proceeds to establish the high probability of several mainland-Greater Antillean faunal connections being the result of over-water dispersal. He concludes by noting the need for improved analyses using cladistic methods and having more complete collections with which to work.

Wilson's analysis is a generally satisfying outline of the geographical history of the West Indian ant fauna. Based on fossil as well as living taxa, dynamic principles involving dispersal and possible radiation *in situ* of certain dispersants, the only discordant element in Wilson's account seems to be the presence of the poor - dispersing Ecitoninae in the fossil record of Hispaniola.

Wilson points out as defects in knowledge of West Indian ants the probable under-collecting of some islands, particularly Cuba and Jamaica, as well as lack of knowledge of certain West Indian taxa that are markedly speciose. To this list of imperfections must be added the absence of phylogenetic analysis of the West Indian ants. Without this information, the details of geographical history of the relatively luxuriant Antillean ant fauna will remain obscure.

Nichols supports the argument that the Greater Antilles function as oceanic islands, using three arguments: first, values derived from Preston's Similarity Index indicate that the islandic scaritine fauna is "in a state of flux": second, the genus *Pasimachus* (adults are large, flightless scaritines) is confined to Middle and North America, with a few species in South Florida and the Yucatan Peninsula: and third, many of the endemic genera of Coleoptera in the West Indies are borers or live under bark. Had there been land connections between the islands and mainland, presumably *Pasimachus* would be represented in the Greater Antilles. Similarly, because a preponderance of endemic and thus older genera of the West Indies live in situations suitable for transport by rafting (*i.e.,* logs) their disproportionate representation in the islands is argument for overseas dispersal. The "state of flux" argument based on the Preston Similarity Index seems to indicate that faunal composition is being determined by forces working on an ecological time scale, and if so, strength is added to Nichols' more general argument. However, the pattern might be an artifact of the method of analysis. As Connor points out (p. 258) this index emphasizes the effects of forces working on an ecological time scale, and these may outweigh historical relationships. Thus, the disturbance of the general order in the fauna implied by its being "in a state of flux" or kaleidoscopic, may not reflect an older underlying reality. Be that as it may, the present pattern of scaritine distribution does seem to me to be rather unordered.

Evidence presented by the vicarists for their hypotheses is interesting but less than convincing. In fact, Hamilton shows, in his phylogenetic reconstruction of the *Polycentropus nigriceps* group (Figs. 7–9, notes G and H, p. 159), that only the terminal clades fit the pattern required by the Rosen model. He concludes that "this cladistic analysis....gives no clear evidence of disjunct inter-island patterns of relationship", and calls for cladistic analyses of other Greater Antillean groups to search for a common pattern. Taken at face value, however, the data presented do not fit the Rosen model, and the author is left in the uncomfortable position of having to question the value of the data presented, thus: "A cladistic analysis of the *nigriceps* group based on the semaphoront [read holomorph] (not just adult male)...would undoubtedly test and enhance the results I have presented here".

Accepting the analysis presented as preliminary, therefore, I would be more encouraged to test the Rosen model further if it were supported by the preliminary data. It seems to me that the pattern of *Polycentropus* is suggestive of inter-island dispersal, and accordingly, it is a dispersalist hypothesis that ought to be tested with a more complete set of data about the species of this genus.

Grimaldi's reconstruction of the geological history of the Greater Antilles calls for a close connection of the proto-Antillean land mass with Africa, following near separation of the former from the American mainland. This seems to be required because of the relationships of some old lineages of Drosophilidae with Old World, rather than with New World, extant lineages. On two counts, I find the argument unconvincing: first, Donnelly's account of Caribbean geological history does not support Grimaldi's hypothesis (in fact, there is no reference to it), and second, just because relicts with African affinities occur in the West Indies, it is not necessary to postulate a direct former connection between the two areas. Puerto Rico could be the last area in the New World where a former widespread lineage has been able to survive. Of the larger Antillean islands, that one is farthest from the mainland, and thus might be expected to accumulate relicts, under the strictures of a dispersalist hypothesis as developed by P. J. Darlington, Jr.

In Liebherr's treatment of *Platynus*, the fauna of each island is discussed, with emphasis on cladistic relationships, and problems therewith. The major problem with the phylogenetic analysis is lack of characters in which one can have confidence. Liebherr recognizes one assemblage (the wingless group) that is based on wing loss (character 40) and displacement of the setae of the posterior angles of the pronotum (character 14). Neither of these features is very reliable as an indicator of relationships, and for the setal feature, this instability is highlighted by the necessity to hypothesize a reversal within the wingless clade, at the base of the *P. jaegeri* group (Figs. 6-7 and 6-8). In that same clade, character 17 (width of pronotal margins) is used to relate the *P. cinchonae* and *P. jaegeri* groups. I have no doubt about the value of this character for determining relationships of similar adjacent allopatric taxa that differentiated comparatively recently, but I am skeptical that such a feature is useful to establish relationships of geographically widely separated clades including a total of 18 species.

Nonetheless, Liebherr uses the hypothesized relationships of the flightless clade in his geographical analysis, suggesting that Rosen's vicariance model "adequately explains taxon relationships among species on Cuba and south and central Hispaniola, and implying that island vicariance and hybridization have been at work along the northern edge of the Caribbean plate". If, in fact, the extreme mobilist hypothesis were established, or if relationships of the *Platynus* species involved in testing the model were more convincingly demonstrated, one would have cause to accept the underlying theory of vicariance biogeography as applied to the West Indies. Under the circumstances, I find little basis for use of Rosen's model in interpreting the history of the West Indian biota.

By accepting at face value the result of the numerical analysis that relates several montane lineages with brachypterous adults, Liebherr is not in a position to consider the possibility that each of these lineages came from lowland winged ancestors which invaded montane habitats on their respective islands, with subsequent extinction of the lowland ancestors and loss of wings among the upland survivors. Such an interpretation may be contrary to the principle of parsimony as practiced by numerical cladists, but the resulting picture might make at least as much sense biogeographically as the interpretation based on the Rosen vicariance model.

Although I am not persuaded of the Rosen model of vicariance nor of the details of relationships and historical interpretation of the distribution pattern of the *Platynus* taxa as presented by Liebherr, I am impressed by the clarity of the presentation and appreciate the value of this contribution in highlighting phylogenetic and zoogeographic areas for further investigation. Discussion of causal relations between brachyptery and diversity, and between climatic change and origin of the bromeliad-inhabiting fauna of Jamaica are insightful, valuable contributions to the more general aspects of West Indian biogeography.

The concluding chapter (No. 11), by Edward F. Connor, outlines mathematically acceptable procedures for inferring historical biogeographic relationships. His principal conclusions are two: first, none of the other authors of this volume used methods acceptable to mathematicians for inferring historical biogeographic relationships: two, "it is best to examine the biogeographical evolution of the Caribbean biota independently of geologic hypotheses concerning area relationships". I suppose that systematists should pay attention to the pronouncements of their more mathematically inclined brethren, and in a logical sense, I can appreciate why one might want to analyze biogeographical data independently of geological hypotheses. However, I believe that, in the absence of the required mathematical precision that plagues most types of biogeographical data, Hennig's principle of reciprocal illumination can be applied to the available geological and phylogenetic biogeographic data, with reasonable approximations to the truth thus being obtained. I suspect it will be more useful for biogeographers to improve the quality of their taxonomic and phylogenetic information than to invest too much effort in elaborate statistical treatment of what is now available.

Connor's negative assessments aside, based on study of this volume I conclude that in view of clear evidence of past crossing of sea barriers by insects, flying or otherwise, and in the absence of clear evidence for the geologic basis of a vicariance hypothesis, little is to be gained by developing a research program to test further the tenets of that hypothesis. Gains are to be made, first by improving the data available for analysis (i.e., more complete collections of the islandic faunas; better information about way of life and local distribution of the species), and second by undertaking phylogenetic analyses of the taxa, to be interpreted using a dispersalist theory, which takes into account the tenets of the theory of island biogeography and the Darlington-Wilson-Erwin theory of taxon cycles or pulses. If such analyses fail

to provide a satisfactory account of the biota and its history, then it will be time to seek other explanatory means.

In conclusion, I found this volume to be enlightening and interesting, and a valuable contribution both to entomology and to the growing knowledge of the West Indian biota. My principal negative comment about the presentation, as such, is the lack of a concluding chapter that could have discussed and perhaps attempted to resolve the different interpretations of biotic history by the various authors. It would have been desirable for each author to have used the same definition of the study area, so that the resulting data could be compared more easily.

This volume ought to be owned and studied by anyone interested in West Indian biogeography. Otherwise, various chapters can be read with profit by taxonomists interested in the taxa treated therein, though not interested in the West Indian fauna, as such.

George E. Ball
Department of Entomology
January, 1989

BOOK REVIEW

IVES, W. G. H. and H. R. WONG. 1988. Tree and shrub insects of the prairie provinces. Information Report NOR-X-292. Northern Forestry Centre, Canadian Forestry Service. Edmonton, Alberta. T6H 3S5. 327 pages, 117 full page colored plates. Available at no charge to persons in the forest industry and educational institutes. ISBN0-662-15770-2.

Even though I am acknowledged in this book as one of the scientific reviewers, my contribution consisted primarily of proof-reading several drafts of computer-processed text that did not at all resemble the very attractive-looking finished product. I feel justified, therefore, in publicly reviewing it, particularly now that I have had a chance to browse through it and, more importantly, to use it. After the title page, the contents are succinctly described in an abstract , which is worth quoting directly,:

"More than 600 species of insects and mites that feed on trees and shrubs in the prairie provinces are discussed in terms of their distribution, hosts, and importance. There are approximately 1100 color photographs; the life cycle and damage of major pest species are illustrated, and for common species, primarily the larval stage is shown. Pests attacking coniferous hosts are separated from those attacking hardwoods, and each group is subdivided according to the type of feeding damage and type of insect involved. An extensive bibliography is provided. In addition to a taxonomic index listing the order and family of each insect and mite, there is a diagnostic index listing the host species, feeding site of the pest, and species of insect or mite involved and an insect index".

Obviously, this is a major scientific work that should appeal to a wide cross-section of users such as students, professional entomologists and ecologists, anyone associated with forestry activities, and even the general public; hopefully, favorable responses from this large audience will generate a lot of good will for the Canadian Forestry Service.

Restrictions of support for insect identification services for provincial agencies prompted the need for this insect guide. However, it took the combined talents of an insect ecologist (W. G. I.) and an insect taxonomist (R. H. W.) to successfully surmount the nomenclatural problems that are bound to arise when dealing with so many species of insects and plants, and to bring together a formidable knowledge of tree and shrub insects of the prairie regions of Canada. No attempt was made to emphasize economically important insects so what we have here is an ecological check list of insects and mites, with descriptions and photographs, associated with native and introduced trees and shrubs of parklands, shelter belts, urban areas of the prairies and parts of the Boreal forest and sub-montane prairie. No claim is made that all insects are included but I believe that a very small proportion have been

missed; after all, both authors have had considerable experience in forest entomology and have had the time to build up large collections, make countless rearings, and record insect occurrences, over many years.

Even a cursory glance at the contents makes it apparent that a tremendous effort went into the production of this book. The two-column layout on standard letter-sized glossy paper is pleasing to the eye and individual species names stand out in bold type. The color plates are on the left hand page and refer only to the species covered on the right hand page, making this one of the easiest to use technical insect identification books I have encountered. All photographs are, in general, faithful renditions of the actual subjects. Text references consist of numbers that refer to items in a bibliography of 657 citations preceding the indices at the end of the book, and are given for species covered in each plate and discussed in the text. I would quibble about the correctness of the word "pest" as it is sometimes used, and I think that the inclusion of a photograph of an adult of a representative looper would have been useful, but these are minor points. The soft covers, though beautifully illustrated on the front with a full color painting of a *Malacosoma disstria* larva, will probably not hold up for very long; in any case, a valuable reference like this should be bound in hard covers.

Unbelievably, there is no charge for this publication. Yet most of my colleagues and myself would have gladly bought it for the $75.00 or so per copy that it took to produce. It is a book to be looked at for its illustrations, read for its interesting biological information, and used as an identification guide. It should be on the bookshelf of every entomologist interested in ecological diversity, the beauty of insects and natural history. recommend it highly.

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Quaestiones

Entomologicae

A periodical record of entomological investigations, published at the Department of Entomology, University of Alberta, Edmonton, Canada.

**TROSIEME CONFERENCE INTERNATIONALE DES
ENTOMOLOGISTES D'EXPRESSION FRANCAISE
Gembloux, 9 - 14 juillet 1990**

Cette conférence - ouverte à tous les entomologistes, arachnologues, acarologues, professionnels ou amateurs de toutes disciplines fondamentales ou appliquées - se tiendra à Gembloux (Belgique) à la Faculté des Sciences agronomiques de l'Etat. Elle donnera lieu à des conférences plénières, communications, tableaux de démonstrations ("posters"), ateliers. Elle comprendra aussi des sessions spéciales dans d'autres villes de Belgique et sera suivie d'excursions.

Les conférences, les différentes communications et ateliers devront s'inspirer du thème général de la conférence:

Méthodes et responsabilités des entomologistes d'aujourd'hui

Les communications s'inscriront dans le cadre de sections qui ont été définies par le Comité organisateur. Elles ne sont pas encore définitives. En voici la liste provisoire:

1. Entomologie culturelle; 2. Entomologie médicale, vétérinaire et médico-légale; 3. Insectes, amateurs et grand public; 4. Entomologie agricole; 5. Entomologie agricole dans les pays en voie de développement; 6. Rôle des arthropodes dans la qualité et la fertilité des sols; 7. Insectes sociaux; 8. Médiateurs chimiques; 9. Entomologie des milieux forestiers; 10. Tendances actuelles de la systématique; 11. Zoogéographie; 12. Systèmes tégumentaires (cuticule, mue et métamorphoses,...).

La langue officielle de la conférence (exposés thématiques, communications et tableaux de démonstrations) sera le français. Cependant les participants auront l'entière liberté de s'exprimer dans la langue de leur choix au cours des discussions qui suivront les exposés ex-cathedra et lors des présentations et discussions des affiches.

Si vous souhaitez participer ou assister aux travaux de l'une ou l'autre des sessions de cette conférence, veuillez rapidement prendre contact ave le Secrétaire général:

Monsieur Charles VERSTRAETEN
Zoologie générale et appliquée
Faculté des Sciences agronomiques de l'Etat
B-5800 Gembloux (P   ique).

Le Comité organisateur

P.S.: Veuillez diffuser cette circulaire autour de vous.

A periodical record of entomological investigation published at the Department of Entomology, University of Alberta, Edmonton, Alberta.

CONTENTS

CLASSIFICATION OF BRAZILIAN SPECIES OF *CICINDELA* AND PHYLOGENY AND BIOGEOGRAPHY OF SUBGENERA *BRASIELLA*, *GAYMARA* NEW SUBGENUS, *PLECTOGRAPHA* AND SOUTH AMERICAN SPECIES OF *CYLINDERA* (COLEOPTERA: CICINDELIDAE)

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ABSTRACT

Brazilian tiger beetles of the tribes Cicindelini, Ctenostomatini, and Megacephalini, subtribes Cicindelina, Odontocheilina and Prothymina, and taxa of the genus Cicindela *are distinguished in identification keys. Diagnoses based on adult characteristics, including genitalia of males and females, new for most species, are provided for four subgenera, 12 species groups, and 29 species of Brazilian* Cicindela. *Species sections consist of nomenclature, recognition, synonyms and types, description, geographical variation, relationships, habitat and period of activity, geographical distribution, lists of localities of examined specimens, distribution map, and figures illustrating taxonomically important external and internal structures.*

A classification of 61 Brazilian and related Neotropical species of Cicindela *is established based on a reconstructed phylogeny employing the methods of Hennig. Brazilian taxa are arranged in sequence according to the reconstructed phylogeny. The four subgenera, species groups, and species recognized are: subgenus* Brasiella *Rivalier,* argentata *group–* C. argentata *Fabricius,* C. obscurella *Klug,* C. pretiosa *Dokhtouroff;* aureola *group–* C. amaenula *Chaudoir,* C. aureola *Klug;* misella *group–* C. dolosula *Rivalier,* C. misella *Chaudoir;* minarum *group–* C. hamulipenis *Horn,* C. brevipalpis *Horn,* C. banghaasi *Horn,* C. minarum *Putzeys; new subgenus* Gaymara *(type species:* C. chlorosticta *Kollar);* chlorosticta *group–* C. chlorosticta *Kollar,* C. staudingeria *Horn,* C. nigroreticulata *Horn, new species* C. paranigroreticulata *(type locality.--Tramandai, Rio Grande do Sul);* anulipes *group–* C. anulipes *Horn; subgenus* Plectographa *Rivalier;* suturalis *group–* C. suturalis *Fabricius,* C. nivea *Kirby;* melaleuca *group–* C. melaleuca *Dejean,* C. patagonica *Brullé;* nigrovittata *group–* C. nigrovittata *Horn;* apiata *group–* C. apiata *Dejean; subgenus* Cylindera *Westwood;* morio *group–* C. kollari *Gistl,* C. confluentesignata

Horn, C. morio *Klug*, C. marquardti *Horn;* friedenreichi *group–* C. piligera *Horn*, C. obsoletesignata *Horn*, C. friedenreichi *Dokhtouroff. Seven new synonymies are proposed with the senior synonym of each combination listed first:* C. argentata argentata *Fabricius* = Brasiliella pseudoargentata *Mandl;* C. obscurella *Klug* = C. obscurella constricta *Rivalier* = Brasiella chrysocollis *Mandl* = Brasiella pallidipes *Mandl;* C. suturalis *Fabricius* = C. trifasciata boliviana *Mandl.*

A reconstructed phylogeny of Cicindela *subgenera which have Brazilian species indicates the following relationships:* Brasiella *as sister group of* Gaymara/Cylindera *lineage,* Gaymara *as sister group of* Plectographa/Cylindera *lineage, and* Plectographa *as sister group of* Cylindera.

Relationships among species groups in each subgenus are indicated as follows: for Brasiella, argentata *group sister of ancestral lineage of sister groups* viridicollis/hemichrysea, aureola *group sister of* cubana/pretiosa *lineage,* misella *group sister of* cubana/horioni *lineage, monobasic* stamatovi *group taxon of uncertain relationships, and* minarum *group sister of* cubana/venezuelensis *lineage; for* Gaymara, chlorosticta *group sister of monobasic* anulipes *group; for* Plectographa, *monobasic* halophila *group taxon of uncertain relationships,* suturalis *group sister of* melaleuca *group, monobasic* nigrovittata *group as taxon of uncertain relationships,* apiata *group sister of* siccalacicola/nigrovittata *lineage; and for* Cylindera, morio *group as sister of* friedenreichi *group.*

Relationships among species of Brasiella *are:* viridicollis *group,* C. cubana *Leng and Mutchler sister of ancestral lineage of sister species* C. acuniai *Mutchler/C.* viridicollis *Dejean,* C. wickhami *Horn sister of* cubana/viridicollis *lineage;* hemichrysea *group,* C. hemichrysea *Chevrolat sister of ancestral lineage of sister species* C. mendicula *Rivalier/C.* sphaerodera *Rivalier;* argentata *group,* C. argentata *Fabricius sister of* venustula/pretiosa *lineage,* C. venustula *Gory sister of ancestral lineage of sister species* C. obscurella *Klug/C.* pretiosa *Dokhtouroff;* aureola *group–* C. rivalieri *Mandl sister of* amaenula/horioni *lineage,* C. amaenula *Chaudoir sister of ancestral lineage of sister species* C. aureola *Klug/C.* horioni *Mandl;* misella *group, ancestral lineage of sister species* C. dolosulaffinis *Mandl/C.* tippmanni *Mandl sister of* dolosula/venezuelensis *lineage,* C. venezuelensis *Mandl sister of ancestral lineage of sister species* C. dolosula *Rivalier/C.* misella *Chaudoir,* stamatovi *group,* C. stamatovi *Sumlin relationships uncertain,* minarum *group,* hamulipenis/banghaasi *lineage sister of* minarum/balzani *lineage,* C. banghaasi *Horn sister of ancestral lineage of sister species* C. hamulipenis *Horn/C.* brevipalpis *Horn,* C. balzani *Horn sister of* minarum/insularis *lineage,* C. minarum *Putzeys sister of* nebulosa/insularis *lineage,* C. nebulosa *Bates sister of ancestral lineage of sister species* C. mandli *Brouerius van Nidek/C.* insularis *Brouerius van Nidek.*

Relationships among Gaymara *species are:* anulipes *group,* C. anulipes *Horn sister to* chlorosticta/paranigroreticulata *lineage;* chlorosticta *group, ancestral lineage of sister species* C. chlorosticta *Kollar/C.* staudingeria *Horn sister of ancestral lineage of sister species* C. nigroreticulata *Horn/C.* paranigroreticulata

n.sp.

Relationships among Plectographa *species:* halophila *group,* C. halophila *Sumlin relationships uncertain;* suturalis *group,* C. siccalacicola *Sumlin sister of* sinuosa/nahuelbutae *lineage, ancestral lineage of sister species* C. sinuosa *Brullé/*C. suturalis *Fabricius sister of* hirsutifrons/nahuelbutae *lineage, ancestral lineage of sister species* C. hirsutifrons *Sumlin/*C. nivea *Kirby sister of ancestral lineage of sister species* C. ramosa *Brullé/*C. nahuelbutae *Peña;* melaleuca *group,* C. mixtula *Horn relationships uncertain, ancestral lineage of sister species* C. ritsemai *Horn/*C. drakei *Horn sister of* melaleuca/chiliensis *lineage, ancestral lineage of sister species* C. melaleuca *Dejean/*C. patagonica *Brullé sister of ancestral lineage of sister species* C. gormazi *Reed/*C. chiliensis *Audouin and Brullé;* nigrovittata *group,* C. nigrovittata *Horn relationships uncertain;* apiata *group,* C. eugeni *Castelnau sister of* C. apiata *Dejean.*

Relationships among South American Cylindera *species:* morio *group, ancestral lineage of sister species* C. kollari *Gistl/*C. malaris *Horn sister of* confluentesignata/marquardti *lineage, ancestral lineage of sister species* C. confluentesignata *Horn/*C. granulipennis *Bates sister of* C. morio *Klug/*C. marquardti *Horn;* friendenreichi *group,* C. friedenreichi *Dokhtouroff sister of ancestral lineage of sister species* C. piligera *Horn/*C. obsoletesignata *Horn.*

The subgenera Brasiella, Gaymara, Plectographa *and* Cylindera *are hypothesized to have originated in western Gondwana prior to the formation of South America. Neotropical diversification within subgenera occurred mainly in the northern half of South America during the Tertiary and Pleistocene. Major centers of species concentration of* Brasiella, Gaymara, *and* Cylindera *are in open country in the eastern and central Brazilian highlands and that of* Plectographa *in northern Argentina. These centers appear to have been long-standing and the chief sources of dispersal during hospitable climatic and geophysical periods, and into which taxa retreated during climatically hostile periods. Important centers of taxa diversification are eastern and southeastern Brazil, northern Argentina and the Amazon River basin. Vegetational changes in the Amazon basin during the Pleistocene appear to have been the major causes of taxa formation.*

RÉSUMÉ

Les cóleoptères Brésiliens de la tribue des Cicindelini, Ctenostomatini, et Megacephalini, du sous-tribue des Cicindelina, des Odontocheilina et des Prothymina, et de la taxa du genre Cicindela *sont classés en groupes distinctes. Les diagnoses, basés sur les caractéristiques des adultes, mâles et femelles inclus, sont nouveaux pour la plupart des espèces et seront donnés pour quatre sous-espèces, 12 groupes d'espèces et 29 espèces de* Cicindela *Brésiliennes. Le classement des espèces est basé, sur une nomenclature, une identification, des listes de synonymes et de types, une description, une variation géographique, les relations, l'habitat et les périodes d'activités, la distribution géographique, les différentes localisations des espèces examinées, une carte des répartitions, et des chiffres illustrant de façon taxonamicale les importantes structures extérieurs et intérieurs.*

Une classification de 61 espèces de Cicindela *Brésiliennes et Neotropicales apparentées est établie grâce a une phylogénie reconstituée en utilisant les méthodes de Hennig. Les taxa* Brésiliennes *sont*

regroupées selon la phylogény reconstituée. Les quartre sous-genres (groupes d'espèces), et les organisations des espèces se font comme suit: sous-genre Brasiella *Rivalier, (groupe* argentata*),* C. argentata *Fabricius,* C. obscurella *Klug,* C. pretiosa *Dokhtouroff, (groupe* aureola*),* C. amaenula *Chaudoir,* C. aureola *Klug, (groupe* misella*),* C. dolosula *Rivalier,* C. misella *Chaudoir, (groupe* minarum*),* C. hamulipenis *Horn,* C. brevipalpis *Horn,* C. banghaasi *Horn,* C. minarum *Putzeys; nouveau sous-genre* Gaymara *(type d'espèces.--*C. chlorosticta *Kollar), (groupe* chlorosticta*),* C. chlorosticta *Kollar,* C. staudingeria *Horn,* C. nigroreticulata *Horn, la nouvelle espèce* C. paranigroreticulata *(type localité.--Tramandai, Rio Grande do Sul), (groupe* anulipes*),* C. anulipes *Horn; sous-genre* Plectographa *Rivalier, (groupe* suturalis*),* C. suturalis *Fabricius,* C. nivea *Kirby, (groupe* melaleuca*),* C. melaleuca *Dejean,* C. patagonica *Brullé, (groupe* nigrovittata*),* C. nigrovittata *Horn, (groupe* apiata*),* C. apiata *Dejean; sous-genre* Cylindera *Westwood, (groupe* morio*),* C. kollari *Gistl,* C. confluentesignata *Horn,* C. morio *Klug,* C. marquardti *Horn, (groupe* friedenreichi*),* C. piligera *Horn,* C. obsoletesignata *Horn,* C. friedenreichi *Dokhtouroff. Sept nouveaux systèmes de synonymes sont proposés avec l'ancien synonyme de chaque combinaisons données auparavent:* C. argentata argentata *Fabricius* = Brasiliella pseudoargentata *Mandl;* C. obscurella *Klug* = C. obscurella constricta *Rivalier* = Brasiella chrysocollis *Mandl* = Brasiliella pallidipes *mandl;* C. suturalis *Fabricius* = C. trifasciata boliviana *Mandl.*

Une phylogénie reconstituée des sous-genres Cicindela *qui comprant les espèces Brésilienne indique les relations suivantes:* Brasiella *comme groupe soeur de la lignée* Gaymara/Cylindera, Gaymara *comme groupe soeur de la lignée* Plectographa/Cylindera, *et* Plectographa *comme group soeur de* Cylindera.

Les relations entre les groupes d'espèces dans chaque sous-genres sont indiquées comme suit: la Brasiella, *le groupe* argentata *soeur de la lignée ancestrale des groupes soeurs* viridicollis/hemichrysea, *le groupe* aureola *soeur de la lignée* cubana/pretiosa, *le groupe* misella *soeur de la lignée* cubana/horioni, *le groupe monobasique* stamatovi *taxon de relations incertaines, et le groupe* minarum *apparenté de la lignée* cubana/venezuelensis; *la* Gaymara, *le groupe* chlorosticta *soeur du groupe monobasique* anulipes; *la* Plectographa, *le groupe monobasique* halophila *taxon de relations incertaines, le groupe* suturalis *soeur du groupe* melaleuca, *le groupe monobasique* nigrovittata *taxon de relations incertaines, le groupe* apiata *soeur de la lignée* siccalacicola/nigrovittata; *et la* Cylindera, *le groupe* morio *soeur du groupe* friedenreichi.

Les relations entre les espèces Brasiella *sont: (groupe* viridicollis*),* C. cubana *Leng et Mutchler soeur de la lignée ancestrale des espèces soeurs* C. acuniai *Mutchler/*C. viridicollis *Dejean,* C. wickhami *Horn soeur de la lignée des* cubana/viridicollis; *(groupe* hemichrysea*),* C. hemichrysea *Chevrolat soeur de la lignée ancestrale des espèces soeurs* C. mendicula *Rivalier/*C. sphaerodera *Rivalier; (groupe* argentata*),* C. argentata *Fabricius soeur de la lignée des* venustula/pretiosa, C. venustula *Gory soeur de la lignée ancestrale des espèces soeurs* C. obscurella *Klug/*C. pretiosa *Dokhtouroff; (groupe* aureola, C. rivalieri *Mandl soeur de la lignée des* amaenula/horioni, C. amaenula *Chaudoir soeur de la lignée ancestrale des espèces soeurs* C. aureola *Klug/*C. horioni *Mandl; (groupe* misella*), la lignée ancestrale des espèces soeurs* C. dolosulaffinis *Mandl/*C. tippmanni *Mandl soeur de la lignée des espèces soeurs* C. dolosula *Rivalier/*C. misella *Chaudoir, (groupe* stamatovi*),* C. stomatovi *Sumlin relations incertaines, (groupe* minarum*), la lignée* hamulipenis/banghaasi *soeur de la lignée des* minarum/balzani, C. banghaasi *Horn soeur de la lignée ancestrale des espèces soeurs* C. hamulipenis *Horn/*C. brevipalpis *Horn,* C. balzani *Horn soeur de la lignée des* minarum/insularis, C. minarum *Putzeys soeur de la lignée* nebulosa/insularis, C. nebulosa *Bates soeur de la lignée ancestrale des espèces soeurs* C. mandli *Brouerius van Nidek/*C. insularis *Brouerius van Nidek.*

Les relations entre les espèce Gaymara *sont: (groupe* anulipes*),* C. anulipes *Horn soeur de la lignée des* chlorosticta/paranigroreticulata; *(groupe* chlorosticta*, la lignée ancestrale des espèces soeurs* C. chlorosticta *Kollar/*C. staudingeria *Horn soeur de la lignée ancestrale des espèces soeurs* C. nigroreticulata *Horn/*C. paranigroreticulata *n.sp.*

Les relations entre les espèces Plectographa: *(groupe* halophila*),* C. halophila *Sumlin relations incertaines; (groupe* suturalis*),* C. siccalacicola *Sumlin soeur de la lignée des* sinuosa/nahuelbutae, *la lignée ancestrale des espèces soeurs* C. sinuosa *Brullé/*C. suturalis *Fabricius soeur de la lignée des* hirsutifrons/nahuelbutae, *la lignée ancestrale des espèces soeurs* C. hirsutifrons *Sumlin/*C. nivea *Kirby soeur de la lignée ancestrale des espèces soeurs* C. ramosa *Brullé/*C. nahuelbutae *Peña; (groupe* melaleuca*),* C. mixtula *Horn relations incertaines, la lignée ancestrale des espèces soeurs* C. ritsemai *Horn/*C. drakei *Horn soeurs de la lignée des* melaleuca/chiliensis, *la lignée ancestrale des espèce soeurs* C. melaleuca *Dejean/*C. patagonica *Brullé soeurs de la lignée ancestrale des espèces soeurs* C. gormazi *Reed/*C. chiliensis *Audouin et Bruellé; (groupe* nigrovittata*),* C. nigrovittata *Horn relations incertaines; (groupe* apiata*),* C. eugeni *Castelnau soeur de* C. apiata *Dejean.*

Les relations entre les Cylindera *d'Amerique du sud: (groupe* morio, *la lignée ancestrale des espèces soeurs* C. kollari *Gistl/*C. malaris *Horn soeur de la lignée des* confluentesignata/marquardti, *la lignée ancestrale des espèces soeurs* C. confluentesignata *Horn/*C. granulipennis *Bates soeur des* C. morio *Klug/*C. marquardti *Horn; (groupe* friendenreichi), C. friedenreichi *Dokhtouroff soeur de la lignée ancestrale des espèces soeurs* C. piligera *Horn/*C. obsoletesignata *Horn.*

Selon une hypothèse les sous-genres Brasiella, Gaymara, Plectographa *et* Cylindera *proviennent de l'ouest du Gondwana avant la formation de l'Amerque du sud. La diversification Neotropicale d'une même sous-genres se trouve surtout dans la partie nord de l'Amerique du sud pendant l'ère Tertiaire et le Pleistocène. Les principaux centers de concentration des* Brasiella, Gaymara, *et* Cylindera *sont la pleine campagne et l'est et central pays de montagnes Brésiliennes et ceux du* Plectographa *en Argentina du nord. Ces centers semblent avoir été pendant longtemps les principaux points de dispersion des périodes climatiques et géophysique hospitalières et de points de retraite pour les taxa durant les périodes hostiles. D'important centers de diversifications des taxa se situent à l'est et au sud-est du Brésil, en Argentine du nord et dans le bassin Amazonien. Les transformations de la végétation du bassin Amazonien pendant le Pleistocène semblant être a l'origine de la transformation des taxa.*

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INTRODUCTION

Brazilian species of *Cicindela* have not been reviewed as a geographical entity, though they have been treated as part of broad systematic works. Horn (1915, 1926a, 1938) in studies of the world fauna established a preliminary classification based mainly on form, colouration, and pubescence of the exoskeleton of adults. He also included synonymies and geographical distributions. In a 'catalogue' on the evolution of *Cicindela*, Schilder (1953) placed almost all Brazilian species into one genus, *Cicindosa* Motschulsky.

Rivalier (1954, 1955) demonstrated relationships among Neotropical species by comparisons of the internal sac of the median lobe, and divided Brazilian forms of *Cicindela* into *Brasiella* Rivalier and *Cylindera* Westwood. Vidal Sarmiento (1966a, b) also conducted studies of female and male genitalia of genera and species of the Cicindelidae of Argentina, but did include some taxa from Brazil.

More recently in a synopsis of the genera of Neotropical Carabidae Reichardt (1977) presented a brief systematic history of *Cicindela*, and recognized nine 'genera' of Rivalier, two of which are principally Brazilian. Sumlin (1979) reviewed Argentine species of *Cicindela* in which a few Brazilian members were noted and included in a key.

Our study was conducted to develop a taxonomic system and historical synthesis for Brazilian and related Neotropical species of *Cicindela*. The following account includes identification keys, descriptions of taxa, classification and evolutionary history. Determinations of species, species groups, and their relationships, are based on external structures, male genitalia as described by Rivalier (1954, 1955) and Vidal Sarmiento (1966b), and female genitalia which are described herein for the first time for most species. Descriptions of male genitalia not studied by Rivalier (1954, 1955) are included.

MATERIALS AND METHODS

This study was based on adults of *Cicindela*, those tiger beetles which occupy open habitats, such as bare patches of soil in grasslands, roads and footpaths, river banks, margins of standing fresh water, and sea beaches. About 1200 adult specimens of Neotropical species of *Cicindela* were examined, including Horn types. W.G. Graham and the senior author collected some specimens in the Manaus area. The great majority of specimens were received on loan from private collections and institutions, for which the following codens after Arnett and Samuelson (1969) and Heppner and Lamas (1982) are used in the text.

BMNH   British Museum (Natural History), Cromwell Road, London, England SW7 5BD.

BRI   Biosystematics Research Institute   C.W. Neatby Bldg. Room 3125,

Research Branch, Ottawa, Ontario, Canada K1A 0C6.

CASC   California Academy of Sciences, Golden Gate Park, San Francisco, California, U.S.A. 94118.

HFHC   Henry H. Howden Collection, Department of Biology, Carleton University, Ottawa, Ontario, Canada K1S 5B6.

ICCM   Carnegie Museum of Natural History, Section of Entomology, 4400 Forbes Avenue, Pittsburgh, Pennsylvania, U.S.A. 15213.

INPA   Instituto Nacional de Pesquisas da Amazonia, Caixa Postal 478, Manuas - 69000, Amazonas, Brazil.

IOC   Instituto Oswaldo Cruz, Rio de Janeiro, Brazil.

IPZE   Akademie der Landwirtschaftswissenschaften der DDR, Institut fur Pflanzenschutzforschung Zweigstelle, Abt. Taxonomie der Insekten, Kleinmachnow, Bereich Eberswalde, 13 Eberswalde-Finow 1, Schicklerstrasse 5, Germany.

LEPC   Luis E. Peña Collection, P.O. Box 2974, Santiago, Chile.

MMKC   Michael M. Kaulbars Collection, Department of Biology, Carleton University, Ottawa, Ontario, Canada K1S 5B6.

MNHP   Museum National d'Histoire Naturelle, Entomologie, 45 rue de Buffon, 75005 Paris, France.

MNRJ   Museu Nacional, Quinta da Boa Vista, Rio de Janeiro, RJ-20,000, Brazil.

MZSP   Museu de Zoologie, Universidade de São Paulo, Avenida Nazare, 481 (Agencia Ipiranga), 04263 São Paulo, SP– Brazil.

RRMC   Robert R. Murray Collection, Fort Worth, Texas, U.S.A. 76107.

USNM   United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. 20560

ZSMS   Zoologische Staatssammlung, Maria-Ward Strasse 1b, D-8000 Munchen 19, Germany.

The various methods and concepts applied in this study have been fairly well established. Structures examined, drawings and measurements, dissections of the male and female genitalia, distribution maps and localities, criteria for species and subspecies, diagnosis of the genus *Cicindela* and reconstruction of phylogenetic system relationships based solely on derived characteristics, have been described elsewhere (Freitag, 1979).

We use special terms that have been applied to features of the male and female genitalia by Rivalier (1954, 1955), Freitag (1965, 1966, 1972), and Vidal Sarmiento (1966a, b, 1967), as shown in Figures 34, 36, 46, 72, 108. A new term, "right bar", is given to a small sclerite which seems to be an extension of the arciform piece on the right side of the internal sac.

Asterisks (*) listed in the Localities sections indicate place names for which the localities are unknown, and an exclamation mark (!) notes that several specimens were examined but that their sex was not determined.

CLASSIFICATION

Notes about taxonomic characteristics

Characteristics common to adults of Brazilian species of *Cicindela* are those typical of the genus (Horn, 1915; Willis, 1968; Freitag, 1979) as well as the following which characterize most species: scape of antenna with one apical seta; tooth of mentum well developed; pronotum with lateral and front portions setose; lateral portions of metasternum and metacoxa setose; procoxa and mesocoxa setose; and elytra with isodiametric microsculpture and apical microserrulations.

Taxa of the Brazilian Cicindelidae

The following keys to the taxa of Brazilian Cicindelidae are constructed from personal examinations of specimens, and diagnostic characteristics given in descriptions, keys and figures by Horn (1915, 1926a, 1938), Rivalier (1954, 1955), Freitag (1966, 1972, 1979), Vidal Sarmiento (1966a, b), Peña (1969), Reichardt (1977), and Sumlin (1979).

Key to Adults of Tribes of Brazilian Cicindelidae

1		Metepisternum narrow, sulcate for entire length; mesepisternum short; lacinia of maxilla without articulated tooth... .... Ctenostomatini
1'		Metepisternum plate-shaped, not entirely sulcate; mesepisternum elongate; lacinia with articulated tooth..................... 2
2	(1')	Pronotum with anterior lateral angles prominent, projected further forward than anterior margin of prosternum, head wide, eyes small; maxillary palpamere 4 in most members of most taxa shorter than maxillary palpamere 3; body without pubescence... Megacephalini
2'		Pronotum with anterior lateral angles not prominent; head with large prominent eyes; maxillary palpamere 4 longer than maxillary palpamere 3; body with pubescence in members of most taxa... Cicindelini

Key to Adults of Subtribes and Subgenera of *Cicindela* of Brazilian Cicindelini

1		Pubescence generally present on head, thorax, and abdomen in members of most taxa; or posterior 0.33 of elytron with pale markings .... subtribe Cicindelina; genus *Cicindela*............... 3
1'		Pubescence generally absent from head, thorax, and abdomen in members of most taxa; posterior 0.33 of elytron without pale markings 2
2	(1')	Elytral epipleuron and free lateral margin of hind coxa glabrous

.... subtribe Prothymina

2'   Elytral epipleuron glabrous or pubescent, and free lateral margin of hind coxa pubescent .... subtribe Odontocheilina

3   (1)   Pale maculations of elytra various, from complete and narrow to reduced and incomplete; labrum tridentate in most species; median lobe of male with apical hook in specimens of most species 4

3'   Pale maculations of elytra broad to extensive in specimens of most species, or depressed, or absent, or discontinuous giving spotted appearance; labrum unidentate or multidentate in specimens of most species; median lobe of male tapered, without hook 5

4   (3)   Body size small, most adults less than 7.5 mm long; labrum with five to 10 (most commonly eight) submarginal setae; pronotum narrow; membrane in place of oviduct sclerite; ventral sclerite of bursa without posterior projections ....
.... subgenus *Brasiella* Rivalier, p. 254

4'   Body size large, most adults 8.0-12.0 mm long (*C. anulipes* is 7.0-7.5 mm); labrum with four to six (seven in a few specimens) submarginal setae; pronotum broad; oviduct sclerite present; ventral sclerite of bursa with setose lateral posterior projections............................ subgenus *Gaymara* n. subg., p. 278

5   (3')   Pale maculations of elytra broad to extensive, or depressed, or absent; head glabrous in specimens of all but one species (gena sparsely pilose in *C. confluentesignata*); thoracic pleuron and sternum glabrous or moderately pilose; labrum unidentate or multidentate; internal sac of median lobe of male lacking dorsal spatulate sclerite............. subgenus *Cylindera* Westwood, p. 317

5'   Pale maculations of elytra well developed in specimens of most species, tendency to be discontinuous, appearance spotted; head with setae (glabrous in *C. suturalis*); thoracic pleuron including proepisternum and sternum densely pilose; internal sac of median lobe of male with dorsal spatulate sclerite......................
.... subgenus *Plectographa* Rivalier, p. 289

Key to the Brazilian species of *Cicindela*

1   Head with setae on either the vertex, frons, clypeus or genae, fine in some specimens and not obvious or abraded 2

1'   Head glabrous (except for one or two supraorbital setae near the inner margin of each eye) 8

2   (1)   Dense appressed setae on vertex, frons, clypeus, genae and most of the rest of the body; elytra completely or almost

without ground colour (Figs. 91a, b); body size 9.0-13.5 mm;
distributed from Espirito Santo, Brazil, south to Argentina ....
....*C. nivea* Kirby, p. 300

2'   Combination of characters not as above.. 3

3   (2')   Body length 8.5-11.0 mm; elytra with ground colour very dark
brown to black, dull, maculations broad, continuous away from
lateral margin, row of large foveae with umbilicate centers near
suture (Fig. 92); distributed in coastal regions in southernmost
portion of Rio Grande do Sul, Argentina, and Chile ....
....*C. melaleuca* Dejean, p. 302

3'   Combination of characters not as above 4

4   (3')   Labrum of most specimens with seven to nine submarginal
setae 5

4'   Labrum of most specimens with fewer than seven submarginal
setae 6

5   (4)   Body length 6.5-7.5 mm; elytra with ground colour brown, dull,
marginal band and apical lunule broad, middle band broad,
oblique (Fig. 32); coupling sulcus of mesepisternum of female
deep round pit; distributed in Matto Grosso................................
....*C. banghaasi* Horn, p. 276

5'   Body length 9.0-10.0 mm; elytra with ground colour brown,
glossy, maculations broad, continous along lateral margin
(Figs. 93a, b); coupling sulcus deep groove; distributed from
Rio Grande do Sul south to Patagonia ....
....*C. patagonica* Brullé, p. 303

6   (4')   Dorsum coppery brown, slightly glossy; elytra with broad and
continuous pale maculations (Figs. 130a-c); genae sparsely
setose, frons and clypeus glabrous; antennae with articles 5-11
pale; labrum with margin irregular, unidentate in most
specimens; in some, seven dentate, with margin incised by
setiferous punctures (Figs. 116a-c); distributed in Minas Gerais,
Uruguay, Argentina, Paraguay ....
....*C. confluentesignata* Horn, p. 319

6'   Combination of characters not as above.. 7

7   (6')   Ground colour dull (matte) black; one or two small pale spots
on elytra (Fig. 94); vertex, frons, and genae sparsely setose;
coupling sulcus of mesepisternum of female shallow, wide,
almost absent; distributed in Minas Gerais.................................
....*C. nigrovittata* Horn, p. 304

7'   Ground colour black (not matte); maculations of elytra reduced
(Figs. 65a-c); vertex, frons clypeus, and genae sparsely setose;
tuft of setae on front inner margin of each eye; coupling sulcus

elongate groove with deep middle; distributed in Rio Grande do
Sul ....*C. paranigroreticulata* new species, p. 287

8   (1')   Labrum edentate or with very small single tooth (Figs. 2, 3, 5)........ 9
8'   Labrum either unidentate or multidentate... 11
9   (8)   Labrum with anterior margin broadly protruded in center (Figs.
            3a-c); elytra dark brown, purplish reflections in few specimens,
            with short wide transverse middle band, small subapical spot of
            humeral lunule present in most specimens, and with subapical
            spot, (Figs. 25a-c); distributed in Amazon basin ....
            ....*C. pretiosa* Dokhtouroff, p. 269
9'   Labrum with anterior margin straight (Figs. 2, 5); pattern of
            elytral markings as in Figures 24, 27... 10
10   (9')   Dorsum bright to dark red-coppery, elytral pattern with humeral
            spot, middle band and subapical spot (Fig. 27); distributed in
            inland southern Brazil..............................*C. aureola* Klug, p. 271
10'   Dorsum black to dark brown; elytral pattern almost effaced
            (Figs. 24a, b); distributed in northern Argentina, Bolivia,
            Paraguay, Uruguay, southern Brazil ....
            ....*C. obscurella* Klug, p. 267
11   (8')   Labrum at least 5-dentate 12
11'   Labrum at most tridentate 15
12   (11)   Body length 6.0 mm; body dull black; labrum indistinctly five
            dentate with six submarginal setae, with middle four setae close
            to margin (Fig. 9); elytron without shoulder, pattern absent
            (Fig. 31); distributed in Matto Grosso, ...
            .... *C. brevipalpis* Horn, p. 276
12'   Combination of characters not as above 13
13   (12')   Ground colour dull brown to black with green head and
            pronotum; elytra with broad apical and humeral lunules (Figs.
            132a, b); tooth of mentum short; labrum 5-dentate (Figs. 118a,
            b); distributed in Matto Grosso .... *C. marquardti* Horn, p. 321
13'   Ground colour black; elytra various, from immaculate to fully
            maculate (Figs. 131, 133); labrum seven to 12 dentate (Figs.
            117, 119); tooth of mentum well developed 14
14   (13')   Elytra with maculations reduced to three spots, each in
            depression, large punctures along suture, large depression in
            basal 0.33 (Figs. 133a, b); articles 5-6 of antenna dark; labrum
            seven dentate with six marginal setae (Figs. 119a, b); coupling
            sulcus of mesepisternum of female in form of groove with
            central pit; distributed in Minas Gerais ....
            ....*C. piligera* Horn, p. 322
14'   Elytra various, from immaculate to fully maculate (Figs.

131a-e); articles five or six of antenna pale; labrum elongate, seven to 12 dentate with eight to 10 marginal setae (Figs. 117a-e); coupling sulcus broad groove; distributed from Amazon River to Matto Grosso .... *C. morio*, Klug, p. 320

15 (11') Elytra with dark lines in form of reticulated pattern against lighter brown and coppery ground colour, humeral lunule short, middle band markedly curved (Figs. 64a, b); labrum unidentate or weakly tridentate with four submarginal setae (Figs. 54a, b); distributed in inland Rio Grande do Sul ....
.... *C. nigroreticulata* Horn, p. 286

15'   Combination of characters not as above 16

16 (15') Head and pronotum deeply rugose and bright coppery with faint green reflections in some specimens; elytra with middle band narrow and strongly oblique as in Figures 62, 63 17

16'   Head and pronotum not deeply rugose and bright coppery; elytra with middle band not oblique 18

17 (16) Body length 8.0-8.5 mm; pattern of elytral maculations as in Figures 62a, b; distributed in central and southeastern Brazil, northeastern Argentina, Paraguay...
.... *C. chlorosticta* Kollar, p. 284

17'   Body length 10.0-12.0 mm; pattern of elytral maculations as in Figures 63a, b; distributed in southeastern Brazil, northern Argentina, Uruguay .... *C. staudingeria* Horn, p. 285

18 (16') Labrum elongate, convex, with three small teeth, and four submarginal setae (Fig. 56); proepisternum with deep and evenly distributed punctures; elytra with reduced maculations (Fig. 66); distributed in Goiás, Matto Grosso, Minas Gerais, Rio Grande do Sul .... *C. anulipes* Horn, p. 288

18'   Combination of characters not as above.. 19

19 (18') Labrum distinctly tridentate (Figs. 1, 4, 6, 7) 20

19'   Labrum unidentate or obscurely tridentate 23

20 (19) Labrum distinctly narrow throughout, central portion of front margin not protruded, central tooth small (Figs. 7a, b); humeral spot of elytron small, on latero-ventral side of shoulder, not evident in dorsal view; distributed in southern Matto Grosso near the Bolivian border, Central America and northwestern South America (probably east of the Andes) south to southwestern Brazil and Argentina..
.... *C. misella* Chaudoir, p. 274

20'   Combination of characters not as above.. 21

21 (20') Elytra slightly glossy brown, maculations broad, middle band slightly oblique (Fig. 26); labrum with broadly rounded teeth,

eight submarginal setae (Fig. 4); distributed inland from Matto Grosso north to Amazon River .... *C. amaenula* Chaudoir, p. 270

21' Elytra dull, brown to black, maculations narrower or more reduced; teeth of labrum narrower (Figs. 1, 6) 22

22 (21') Elytron with humeral spot, subhumeral spot distinct (Figs. 23a-e); small bell-shaped unpigmented area on posterior margin of sternum 5 of females distributed from Brazil north to Mexico, south to Argentina .... *C. argentata* Fabricius , p. 265

22' Elytron with humeral spot absent, subhumeral spot tiny (Fig. 28); bell-shaped unpigmented area on posterior margin of sternum 5 of females absent; distributed from eastern Brazil west to Colombia .... *C. dolosula* Rivalier, p. 273

23 (19') Elytra with pale maculations widely expanded, continuous in some specimens, humeral lunule oblique, punctation very large and deep (Figs. 129a, b); articles 5-11 of antennae pale; body pubescence moderately dense; labrum distinctly unidentate with five or six sub-marginal setae (Figs. 115a, b); distributed in central Brazil .... *C. kollari* Gistl, p. 317

23' Combination of characters not as above 24

24 (23') Elytra black, maculations obsolete and depressed, with broad punctures near median suture and shoulders (Fig. 134); labrum unidentate, dark at base, six submarginal setae (Fig. 120); distributed in Santa Catarina, northern Argentina .... *C. obsoletesignata* Horn, p. 323

24' Combination of characters not as above 25

25 (24') Body length 6.0 mm; elytra dull dark brown, maculations largely effaced (Fig. 30); labrum unidentate with five to seven submarginal setae (Fig. 8); distributed in Goiás .... *C. hamulipenis* Horn, p. 275

25' Combination of characters not as above 26

26 (25') Elytra with maculations complete and continuous or broad (Figs. 90, 95) 27

26' Elytra with maculations reduced (Figs. 33, 121) 28

27 (26) Elytra with ground colour dull dark brown, maculations broad, lacking marginal band (Figs. 95a-d); labrum unidentate, tooth prominent, or obscurely tridentate, seven to 13 submarginal setae (Figs. 83a-d); coupling sulcus of mesepisternum of female broad groove; distributed in coastal and inland Rio de Janeiro, Minas Gerais, Matto Grosso, Rio Grande do Sul, northern Argentina .... *C. apiata* Dejean, p. 305

27' Elytra with ground colour glossy, with coppery, green and blue (in some specimens) reflections, maculations complete and

continuous, middle band sinuate (Figs. 90a-e); labrum unidentate, with 8-10 submarginal setae (Figs. 78a-e); coupling sulcus deep sinuate groove; distributed from southern Brazil north to Trinidad and southern Caribbean Islands......................
....*C. suturalis* Fabricius, p. 298

28   (26')   Elytra dull, black, apical lunule with recurved hook at distal end (Figs. 33a, b); labrum short almost tridentate, with seven to 12 submarginal setae (Figs. 11a, b); coupling sulcus of mesepisternum of female deep groove with central pit; distributed in Espirito Santo, Minas Gerais, Matto Grosso, São Paulo ....*C. minarum* Putzeys, p. 277

28'   Elytra slightly glossy, black, middle band, especially apical end, depressed (Figs. 135a, b); labrum unidentate with seven of eight setae almost marginal (Figs. 121a, b); coupling sulcus long sinuate groove; distributed in Rio Grande do Sul, Santa Catarina ....*C. friedenreichi* Dokhtouroff, p. 324

Subgenus *Brasiella* Rivalier

Genus *Brasiella* Rivalier, 1954: 261 (TYPE SPECIES, *Cicindela argentata*, by iginal designation). Rivalier, 1955: 79. Reichardt, 1977: 374.
Brasiliella Mandl, 1963: 581; 1973: 270 (incorrect subsequent spelling).

Recognition.— Adults of this subgenus are distinguished by the five characters given in couplet 4 of the key. In addition the head is glabrous (except for *C. banghaasi*); labrum tridentate, unidentate, edentate, or indistinctly five dentate; pale maculations of elytra are complete and narrow in most species or reduced or completely absent; middle of abdominal sterna pubescent; apex of median lobe of the male is hooked in most species, and central plate and flagellum are absent in the internal sac; the spermatheca and duct of the female together are approximately 1.0-1.5 mm long.

Species groups.— This subgenus has seven species groups that include 29 species. Six groups are found in South America, of which four are in Brazil, *argentata* group, *aureola* group, *misella* group, and *minarum* group.

Geographical distribution.— The geographical range of this subgenus extends from northern Argentina northward to southwestern United States and the West Indies. In Brazil most taxa in this subgenus are concentrated south of the Amazon River in the Brazilian Highlands and southern parts of the Amazon basin.

Phylogenetic relationships.— Subgenus *Brasiella* is sister to the lineage that gave rise to subgenera *Gaymara, Plectographa*, and *Cylindera*.
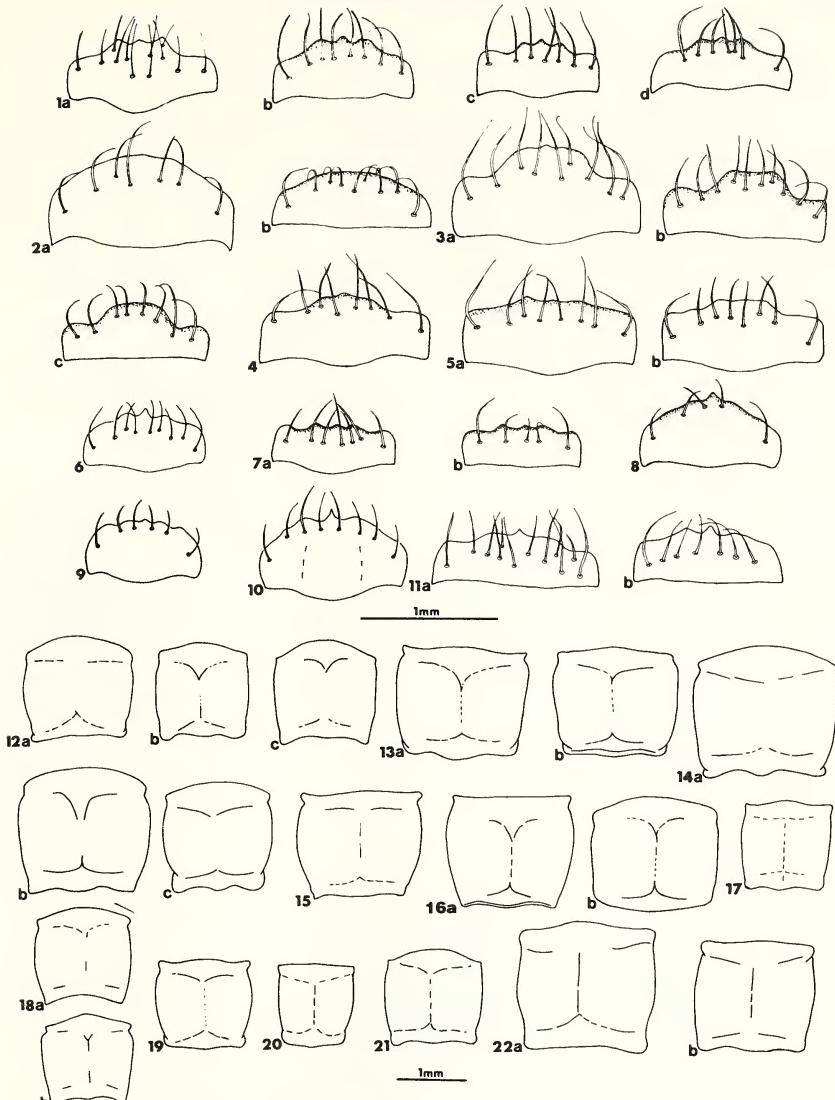
Figs. 1–11. Labrum, dorsal aspect. 1, *Cicindela argentata* Fabricius: (a) female, Estac, S.P.; (b) female, Ypiranga, S.P.; (c) male, Arinos, M. Gerais; (d) male, 40 km w. Manaus, Am.; 2, *C. obscurella* Klug, Montevideo, Uruguay: (a) female; (b) male; 3, *C. pretiosa* Dokhtouroff, Manaus, Am.: (a) female; (b), (c) male; 4, *C. amaenula* Chaudoir, female, near Amazon River; 5, *C. aureola* Klug, female: (a) São Paulo, S.P.; (b) Vacaria, M. Grosso; 6, *C. dolosula* Rivalier, male, Chapada, Go.; 7, *C. misella* Chaudoir, Bugaba, Colombia: (a) female; (b) male; 8, *C. hamulipenis* Horn, male, Dianopolis, Go.; 9, *C. brevipalpis* Horn, male, Vacaria, M. Grosso; 10, *C. banghaasi* Horn, female, Cuyaba, M. Grosso; 11, *C. minarum* Putzeys: (a) female, Vacaria, M. Grosso; (b) male, Espirito Santo. Figs. 12–22. Pronotum, dorsal aspect. 12, *C. argentata* Fabricius: (a) female, Ypiranga, S.P.; (b) male, Arinos, M. Gerais; (c) male, 40 km w. Manaus, Am.; 13, *C. obscurella* Klug, Montevideo, Uruguay: (a) female; (b) male; 14, *C. pretiosa* Dokhtouroff, Manaus, Am.: (a) female; (b), (c) male; 15, *C. amaenula* Chaudoir, female, near Amazon River; 16, *C. aureola* Klug, female: (a) São Paulo, S.P.; (b) Vacaria, M. Grosso; 17, *C. dolosula* Rivalier, male Chapada, Go.; 18, *C. misella* Chaudoir, Bugaba, Columbia: (a) female; (b) male; 19, *C. hamulipenis* Horn, male, Dianopolis, Go.; 20, *C. brevipalpis* Horn, male, Vacaria, M. Grosso; 21, *C. banghaasi* Horn, female, Cuyaba, M. Grosso; 22, *C. minarum* Putzeys; (a) female, Vacaria, M. Grosso; (b) male, Espirito Santo.
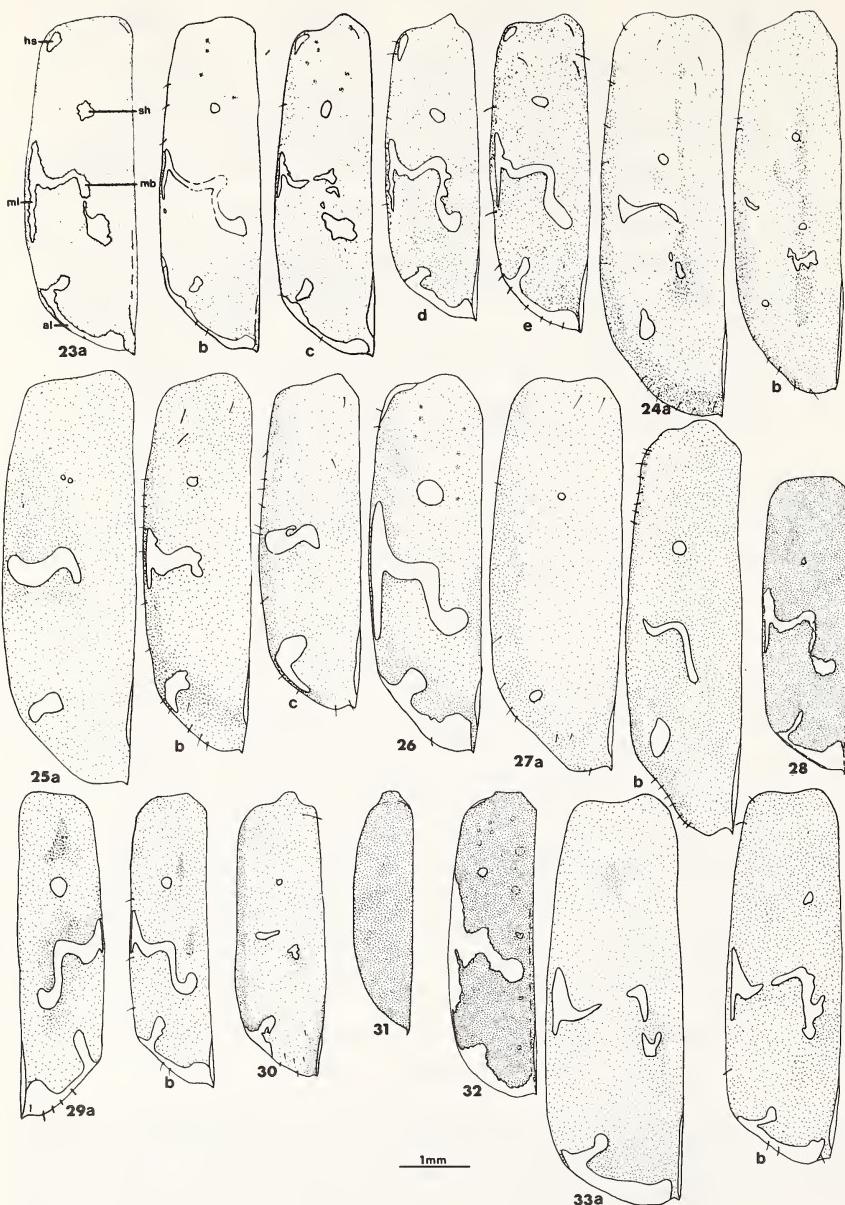
Figs. 23–33. Elytron, dorsal aspect. 23, *Cicindela argentata* Fabricius; (a) female, Estac, S.P., apical lunule (*al*), humeral spot (*hs*), middle band (*mb*), marginal band or lunule (*ml*), subhumeral spot (*sh*); (b), (c), female, Ypiranga, S.P.; (d) male, Arinos, M. Gerais; (e) male, 40 km w. Manaus, Am.; 24, *C. obscurella* Klug, Montevideo, Uruguay: (a) female; (b) male; 25, *C. pretiosa* Dokhtouroff, Manaus, Am.: (a) female; (b), (c) male; 26, *C. amaenula* Chaudoir, female, near Amazon River; 27, *C. aureola* Klug, female: (a) São Paulo, S.P.; (b) Vacaria, M. Grosso; 28, *C. dolosula* Rivalier, male, Chapada, Go.; 29, *C. misella* Chaudoir, Bugaba, Colombia: (a) female; (b) male; 30, *C. hamulipenis* Horn, male, Dianopolis, Go.; 31, *C. brevipalpis* Horn, male, Vacaria, M. Grosso; 32, *C. banghaasi* Horn, female, Cuyaba, M. Grosso; 33, *C. minarum* Putzeys: (a) female, Vacaria, M. Grosso; (b) male, Espirito Santo.
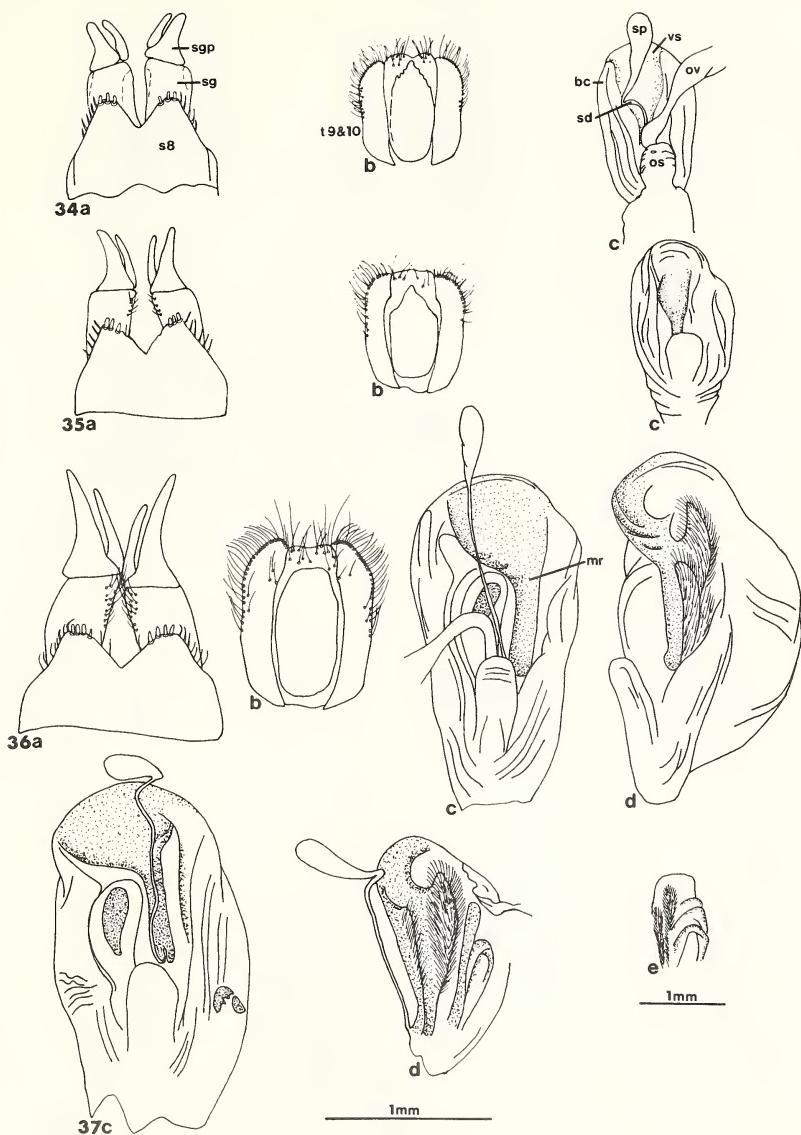
Figs. 34–37. Female genitalia: (a) sternum 8 (*s8*), second gonocoxa (*sg*), second gonapophyses (*sgp*), ventral aspect; (b) syntergum 9 and 10 (*t9&10*), dorsal aspect; (c) bursa copulatrix (*bc*), median ridge (*mr*), oviduct sclerite (*os*), oviduct (*ov*), spermatheca (*sp*) and duct (*sd*), ventral sclerite (*vs*), ventral aspect; (d) bursa copulatrix left lateral aspect; (e) bursa copulatrix dorsal aspect. *Cicindela argentata* Fabricius: 34, Estac, S.P.; 35, Ypiranga, S.P.; 36, 37, *C. obscurella* Klug, Montevideo, Uruguay.
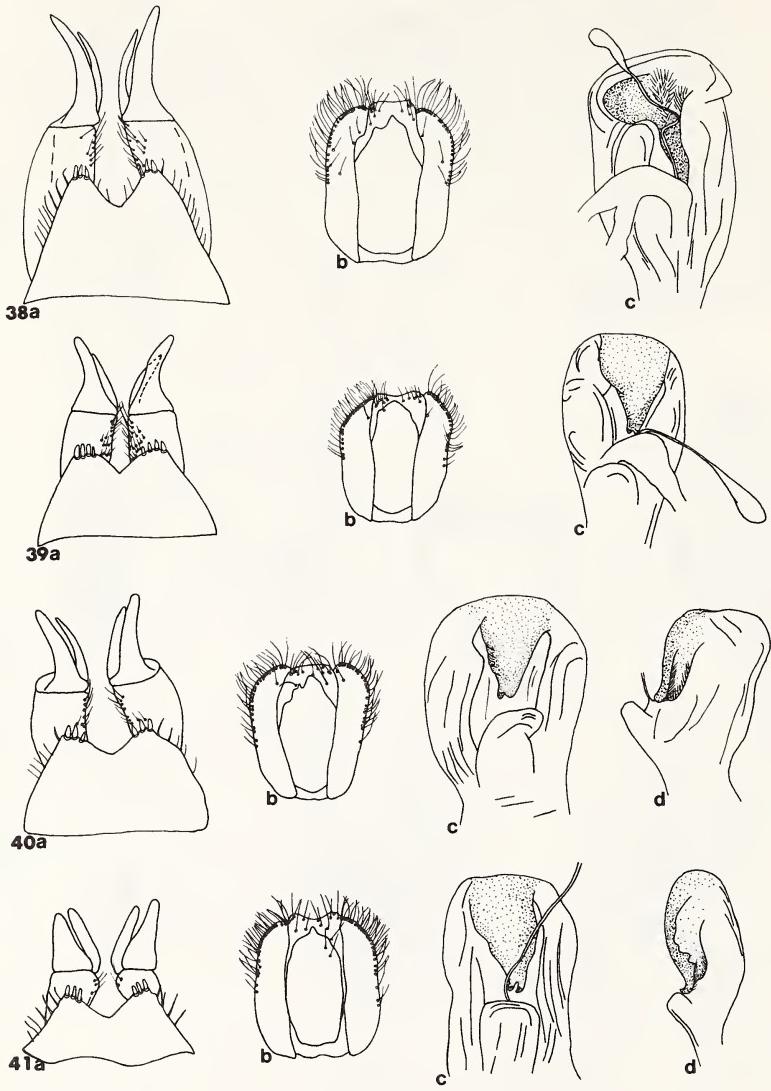
Figs. 38–41. Female genitalia: (a) sternum 8, second gonocoxa, second gonapophyses, ventral aspect; (b) syntergum 9 and 10, dorsal aspect; (c) bursa copulatrix, median ridge, oviduct sclerite, oviduct, spermatheca and duct, ventral sclerite, ventral aspect; (d) bursa copulatrix left lateral aspect. 38, *Cicindela pretiosa* Dokhtouroff, Manaus, Am; 39, *C. amaenula* Chaudoir, near Amazon River; *C. aureola* Klug, 40, São Paulo, S.P.; 41, Vacaria, M. Grosso.
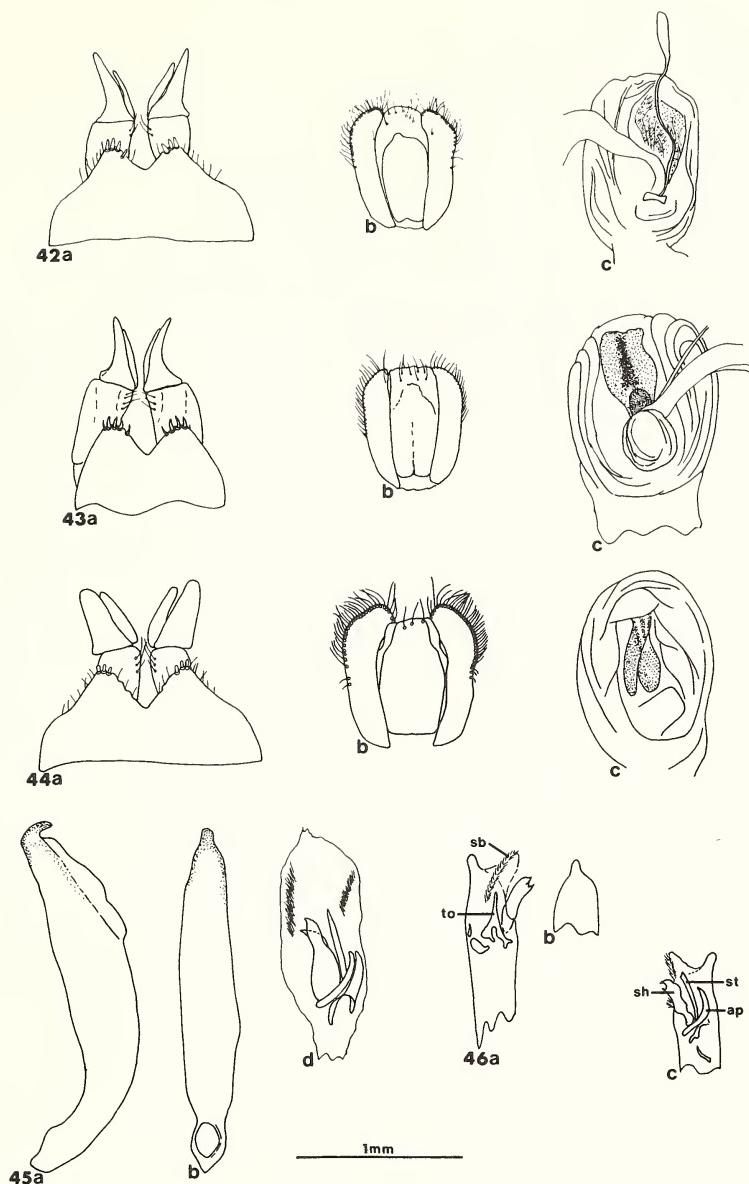
Figs. 42–44. Female genitalia: Female genitalia: (a) sternum 8, second gonocoxa, second gonapophyses, ventral aspect; (b) syntergum 9 and 10, dorsal aspect; (c) bursa copulatrix, median ridge, oviduct sclerite, oviduct, spermatheca and duct, ventral sclerite, ventral aspect. 42, *Cicindela misella* Chaudoir, Bugaba, Columbia; 43, *C. banghaasi* Horn, Cuyaba, M. Grosso; 44, *C. minarum* Putzeys, Vacaria, M. Grosso. Figs. 45–46. Male genitalia: median lobe (a) right lateral aspect; (b) dorsal aspect; (c) left lateral aspect; (d) internal sac, arciform piece (*ap*), setal brush (*sb*), shield (*sh*), stylet (*st*), tooth (*to*). 45, *C. hamulipenis* Horn, Dianopolis, Go.; 46, *C. brevipalpis* Horn, Vacaria, M. Grosso.

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Fig. 47. Map showing the geographical distribution of the species *Cicindela argentata* Fabricius. Open circles represent state records.

Fig. 48. Map showing the geographical distribution of the species *Cicindela obscurella* Klug (●), and *C. pretiosa* Dokhtouroff (■). Open circles represent state records of *C. obscurella* Klug.

Fig. 49. Map showing the geographical distribution of the species *Cicindela amaenula* Chaudoir (●), and *C. aureola* Klug (■). Open circle and square represent state record for *C. amaenula* Chaudoir and *C. aureola* Klug respectively.

Fig. 50. Map showing the geographical distribuiton of the species *Cicindela dolosula* Rivalier (●), and *C. misella* Chaudoir (■). Open circle and square represent state records for *C. dolosula* Rivalier, and *C. misella* Chaudoir respectively.

Fig. 51. Map showing the geographical distribution of the species *Cicindela hamulipenis* Horn (●), *C. brevipalpis* Horn (■), *C. banghaasi* Horn (▲), and *C. minarum* Putzeys (▼).

The *argentata* group

Adults of this group are characterized by elytral foveae not obvious, and unpigmented bell-shaped spot on abdominal sternum 5 of the female. The group has four species, three of which are found in Brazil, *C. argentata, C. obscurella,* and *C. pretiosa.* The geographical range of the *argentata* group extends from northern Argentina northward to northern South America and the Lesser Antilles. The *argentata* group is a close relative of the *viridicollis* and *hemichrysea* groups.

Cicindela (Brasiella) argentata Fabricius
Figs. 1, 12, 23, 34, 47

Cicindela argentata argentata Fabricius, 1801: 242 (TYPE LOCALITY, in America meridionali). - Herbst, 1806: 208. - Dejean, 1825: 147; 1831: 215. Kirsch, 1873: 125. - Bates, 1881: 14. - Horn, 1896a: 354; 1903: 334; 1904: 86; 1906: 87-91; 1915: 406; 1923: 111; 1926a: 308; 1938: 52. Varas Arangua, 1925: 37. - Barattini, 1929: 1218. - Blackwelder, 1944: 17. - Cazier, 1954: 286. - Rivalier, 1954: 261-263; 1955: 79-80; 1970: 857. Brouerius van Nidek, 1956: 320. - Mandl 1956: 389; 1963: 581; 1964: 16; 1967: 437, 439; 1973: 290. Vidal Sarmiento, 1966a: 256-257; 1966b: 32-33. - Balazuc and Chalumeau, 1978: 22. - Sumlin, 1979: 102.

Cicindela guerin Gory, 1833: 178 (TYPE LOCALITY, Cayenne). - Horn, 1896a: 354; 1915: 406; 1926a: 308. - Blackwelder, 1944: 17.

Cicindela lucorum Gistl ,1837: 71 (TYPE LOCALITY, in Cayenna). - Horn, 1915: 406; 1926a: 308. - Blackwelder, 1944: 17.

Cicindela egaensis Thomson, 1857: 130 (TYPE LOCALITY, Ega, Amazone supér.).) - Horn, 1915: 406; 1926a: 308. - Blackwelder, 1944: 17.

Brasiliella pseudoargentata Mandl, 1963: 582 (TYPE LOCALITY, Jacaré P.N. Xingu, M. Grosso, Bras.). NEW COMBINATION AND SYNONYMY.

Cicindela argentata pallipes Fleutiaux and Sallé, 1889: 359 (TYPE, sex undetermined, in the MNHP general collection bearing the following label: "Guadeloupe Delauney/*C. argentata* F., v. *pallipes* (ch²)/Museum Paris Box collection Fleutiaux/Type" (black letters on red label); (TYPE LOCALITY, Guadeloupe). -Horn, 1903: 334; 1915: 406;1926a: 308. - Leng and Mutchler, 1916: 696. - Blackwelder, 1944: 17. - Rivalier, 1955: 80.

Cicindela argentata umbrogemmata Horn , 1906: 87 (TYPE LOCALITY, Posorja, Ecuador (Campos)); 1915: 407; 1926a: 308; 1938: 52. –Blackwelder, 1944: 17.

Cicindela argentata macella Rivalier , 1955: 80 (TYPE, a male in the MNHP general collection bearing the following label: "Muséum Paris de la Mana Leschor/ penis 873 Rivalier/*argentata* s.s. *macella* mihi. E. Rivalier det/TYPE" (black letters on red label); TYPE LOCALITY, Brésil).

Cicindela argentata semicircumscripta Mandl , 1958: 23 (TYPE LOCALITY, Santiago del Estero, El Pinto). - Sumlin, 1979: 103.

Cicindela argentata ecuadorensis Mandl , 1973: 290 (TYPE LOCALITY, Ecuador, San Anton. Curaray).

Recognition.— Specimens of *C. argentata* are distinguished from those of the similar species *C. obscurella* by a combination of the following characteristics: in most specimens maculations of elytra well developed with complete marginal band and humeral spot, subapical spot and apical lunule (Figs. 23a-e); labrum of average length and obsoletely to strongly tridentate with middle tooth well developed in most specimens (Figs. 1a-d); sides of inside of bursa copulatrix in females lightly sclerotized and brushes of setae absent (Figs. 34c, 35c). In addition, the shapes of the sclerites of the internal sac of the median lobe of the two above species differ (Rivalier, 1955: 81,84; Vidal Sarmiento, 1966b: 33). Also see Recognition section

for *C. misella* and *C. dolosula*.

Synonyms and Types.— We have not seen types of the *C. argentata* complex except for that of *C. argentata macella* Rivalier and *C. argentata pallipes* Fleutiaux and Sallé. Names are based upon comparison of original descriptions with specimens on loan. Rivalier (1955: 80) is correct in stating that *C. taitiensis* Boheman is a cicindelid from Tahiti which is not an element of the American fauna. The name *C. pseudoargentata* Mandl has been assigned to small specimens of *C. argentata*.

Description.—

Body length. 6.0-8.0 mm M and F.

Body color. Head, pronotum and elytra dull to slightly glossy, black to coppery brown, elytra of some specimens with green reflections. Venter, pleuron and sides of head with green, blue, and coppery reflections.

Body setae. Proepisternum and mesepisternum sparsely setose, metepisternum more densely setose; lateral margins of abdominal sterna 1-6 setose.

Other external features. Labrum of average length, tridentate, with eight submarginal setae, ranging in number from five to 12 (Figs. 1a-d). Pronotum narrow, sutures shallow (Figs. 12a-c). Coupling sulcus of female shallow to moderately deep groove, with deeper pit in middle. Apex of front trochanters with one seta. Apices of elytra slightly to not recurved. Pattern of elytral maculations with humeral lunule discontinuous, humeral spot on shoulder in most specimens, humeral subapical spot present; marginal band in most specimens; middle band complete or discontinuous; apical lunule complete or discontinuous (Figs. 23a-e). Punctures of elytra large, shallow, with green (mainly) and coppery reflections.

Female genitalia. Sternum 8 with deep and broad V-shaped posterior emargination; apices moderately rounded, each with three short stout setae (Figs. 34a, 35a). Second gonapophyses broad, medial portion almost as long as lateral portion (Figs. 34a, 35a). Syntergum 9 and 10 as in Figures 34b, 35b. Ventral sclerite broad, lightly sclerotized, median ridge absent; inside lateral walls of bursa slightly sclerotized (Figs. 34c, 35c). Thick membrane in place of oviduct sclerite (Figs. 34c, 35c). Length of spermatheca and duct *ca* 1.0 mm. See also Vidal Sarmiento (1966a; 256).

Male genitalia. Male genitalia have been described by Rivalier (1955: 81) and Vidal Sarmiento (1966b: 33).

Geographical Variation and Subspecies.— Variable elytral maculations include the humeral spot almost absent or very well marked, and marginal band absent or reduced (few specimens) or well marked (most specimens). The middle band is discontinuous in some specimens. A complete apical lunule is the general condition, though a few specimens with a discontinous one are present throughout the species range. Geographical patterns in these characteristics are not clearly discernible, though maculations of the elytra are broader and more frequently complete in specimens from northern Brazil. Specimens in southern Brazil tend to have discontinuous or absent portions of the elytral maculations. Specimens of *C. a. macella* Rivalier have elytral maculations much reduced. Whether or not they are the predominant form in well defined geographical populations remains to be seen. We follow recent authors in recognizing subspecies of non-Brazilian forms.

Relationships.— *Cicindela argentata* is sister to the lineage that gave rise to *C. venustula* Gory (northern S. America) and sister species *C. obscurella* and *C. pretiosa*.

Habitat and Period of Activity.— Label data indicate a period of activity from December to April. Adults live in moist open areas in grassy vegetation. They

occasionally occur along river beaches but usually near clumps of grass (Pearson, 1984).

Geographical Distribution, Localities, Examined Specimens.— Inland and near coasts, from northern Argentina, Uruguay to northern Brazil and French Guiana (Fig. 47), and Guadeloupe.

Argentina. *Cordoba*: no locality, 1M, MZSP. *Formosa*: Guaycolec, 2F, MZSP. *La Rioja*: Patquia, 1M, 1F, MZSP. *Tucuman*: no locality, 1M, 1F, MZSP.

Bolivia. Prov. del Sara*, 6M, 9F, ICCM; Santa Cruz de la Sierra Bol., 1M, ICCM.

Brazil. *Amazonas*: Arima (on Rio Purus), 1M, ICCM; Beruri (on Rio Purus), 4M,5F,MZSP; Canindé (50 km e), 4M, 3F,MZSP; Hyutanaham (on Rio Purus), 31M, 18F, ICCM; Itacoatiara (30 km w. on Rio Urubu), 2F, ICCM; Manaus, 3M, 4F, INPA; Manaus (Reserva Ducke, km 26 on Itacoatiara Hwy), 1M, BRI; Manaus (30 km ne), 3M, INPA; Manaus (40 km w. at Lago Janauaca), 1M, BRI; Manaus (60 km n), 1M INPA; Rio Cavaburi, 3F, MZSP; Rio Prêto, 1M, MZSP; Santo Antonio do Iga, 1F, MNRJ; São Gabriel, 1M 2F, IOC; Tapuruquara (on Rio Negro), 1F, MZSP; Tefé, 1F IOC. *Ceará*: Aracati, 1F, MZSP; IOC, 1M, 1F, MZSP; Jaquaribe, 1M, MZSP; Russas, 1M, 2F, MZSP. *Espirito Santo*: Guandu*, 1M, 1F, IOC; no locality 1F, MNRJ. *Goiás*: Cabeceiras (Lagos Formosa), 1M, 2F, MZSP; Chapada, 6M, 6F, ICCM; Jatai, 17M, 6F, MZSP; Pirineus*, 1F, MZSP; Vianopolis, 1F, MZSP. *Matto Grosso*: Barra do Tapirapé, 3M, 1F, MZSP; Bodoquena, !, IOC; Camisao*, 1F, MZSP; Corumba, 1M, MZSP; Jacaré Pq. Nac. Xingu, 1M, MZSP; Murtinho*, 1M, MZSP; Vacaria, 6M, 1F, MZSP; Salobra (Rio?), !, IOC; Três Lagoas, 1M, MZSP; Urucum, 1F, MZSP, 1M, MNRJ; Xingu, 1M, MZSP. *Minas Gerais*: Buritis, 1M, 1F, MZSP; Ipatinga, 1M, MZSP; Mar de Espanha*, 1M, MZSP; no locality, 1F, MZSP; Serra Caraca, 1F, MZSP. *Pará*: Cachimbo, !, IOC, 12!, MZSP; Oriximina, 2M, 2F, MZSP; Santarem, 7M, 5F, ICCM. *Paráiba*: Corema, 1M, MZSP. *Paraná*: Ponta Grossa, 1M, 1F, MZSP. *Santa Catarina*: Joinville, 1M, MZSP; Nova Teutonia, 2M, 1F, MZSP. *São Paulo*: Alto da Serra*, 1M, MZSP, Avanhand (Garbe Lake)*, 1M, MZSP; Barueri, 4M, 5F, MZSP; Boraceia*, 1M, 3F, MZSP; Campos do Jordao, 1F, MZSP; Cantareira, 1F, MZSP; Caraquatatuba, 1F, MZSP; Embu, 1F, MZSP; Estac, 1F, MZSP; Iporanga, 3F, MZSP; Itu, 2M, MZSP; Mairiporã, 1M, MZSP; 1M, MZSP; Onda Verde*, !F, MZSP; Pindamonhangaba, 1M, 1F, MZSP. Pirassununga, 1M, MZSP; Rincao, 1M, MZSP; São Paulo, 2M, 2F, MZSP; Sapuchui, 1M, MZSP; Ypiranga, !, MZSP.

French Guiana. Oiapoque River, 3M, 5F, ICCM.

Paraguay. Asuncion, 2F, ICCM.

Peru. Huancayo, !, IOC; Rio Ampiacu*, 1M, 1F, MZSP.

Uruguay. Paysandu (on Rio Uruguay), 1M, MNRJ.

(Note: Ecuador; *C. a. umbrogemmata* Horn, 1906: 87.

Venezuela; *C. argentata* and *C. a. pallipes* Horn, 1903: 334.

Cicindela (Brasiella) obscurella Klug
Figs. 2, 13, 24, 36, 37, 48

Cicindela obscurella Klug, 1829: 3 (TYPE LOCALITY, Süd-Brasilien). - Dejean, 1831: 268. - Horn, 1891: 324; 1906: 89; 1915: 407; 1926a: 308; 1938: 52. - Barattini, 1929: 1219. - Fernandez, 1936: 105. - Blackwelder, 1944: 17. - Rivalier, 1954: 263; 1955: 82. Vidal Sarmiento, 1966a: 256-257; 1966b: 32. Sumlin, 1979: 103.

Cicindela tripunctata Dejean , 1831: 267 (TYPE LOCALITY, les parties meridionales du Brésil). - Horn, 1915: 407; 1926a: 308. Blackwelder, 1944: 17. - Vidal Sarmiento, 1966b, 32.

Cicindela celeripedestris Horn, 1896b: 357 (TYPE LOCALITY, Minas Geraes); 1938: 52. Blackwelder, 1944: 17. - Rivalier, 1955: 84. Vidal Sarmiento, 1966b: 32.

Cicindela obscurella constricta Rivalier, 1955: 83 (TYPE, a male in the MNHP general collection bearing the following labels: "Brésil (Minas) Sertao de Diamantina Faz Das Melancias E. Gounelle 10-11 1902/Muséum Paris Brésil coll. E. Gounelle 1913/ *B. obscurella* ssp. *constricta* mihi E. Rivalier det/TYPE" (black letters on red label)/ "penis 974 Rivalier"; TYPE LOCALITY, Minas Geraes). NEW SYNONYMY.

Brasiliella chrysocollis Mandl, 1963: 585 (TYPE LOCALITY, Jacare P.N. Xingu, M. Grosso, Bras.). NEW COMBINATION AND SYNONYMY.

Brasiliella pallidipes Mandl, 1963: 589 (TYPE LOCALITY, Sta. Catarina, Brasil). NEW COMBINATION AND SYNONYMY.

Recognition.— The elongate and edentate labrum (Figs. 2a, b) combined with the almost effaced elytral maculations. (Figs. 24a, b) separates *C. obscurella* from other species of the *argentata* group. Adults of *C. obscurella* are generally larger than adults of its sister species *C. argentata*. Two dark finger-like brushes of setae in the bursa copulatrix of females also distinguish *C. obscurella* from other related species (Figs. 36d, 37d, e). In addition the shapes of sclerites in the internal sac of the median lobe of males characterize this species (Rivalier, 1955: 84).

Synonyms and Types.— Except for the holotype and allotype of *C. o. constricta* Rivalier, we have not seen the types of this complex. The names are based on comparison of original descriptions with specimens on loan.

In treating *C. celeripedestris* Horn as a junior synonym we follow Horn (1938: 53) and Vidal Sarmiento (1966b: 32). We have examined specimens from Uruguay which conform to the description of *C. o. constricta* Rivalier. They do not appear to form a single geographical population. *Brasiliella chrysocollis* Mandl appears to be a coloured form of *C. o. constricta* Rivalier. We consider *Brasiliella pallidipes* Mandl to be a small form of *C. obscurella* in view of the fact that the labrum is edentate and that it is found within the range of *C. obscurella*.

Description.—

Body length. 8.0 mm M, 8.5 mm F.

Body colour. Head and pronotum slightly glossy, black with coppery reflections; elytra dull, black with coppery reflections, some specimens with green, blue or purple reflections. Venter glossy, black with green, blue, purple and coppery reflections; pleuron mainly coppery, green and blue.

Body setae. Pronotum and proepisternum sparsely setose, mesepisternum with a few setae at ventral end, metepisternum more densely setose; abdominal sterna one to six setose mainly on lateral margins.

Other external features. Labrum elongate edentate, median portion almost tooth-like in some females, with eight submarginal setae, ranging in number from six to 10 (Figs. 2a, b). Pronotum narrow, sutures shallow (Figs. 13a, b). Coupling sulcus of mesepisternum of female a long and sinuate groove. Apex of front trochanters with one sensory seta, middle of trochanters glabrous. Elytra with recurved apices; maculations discontinuous or almost effaced; punctures large, shallow, with green (mainly) and coppery reflections (Figs. 24a, b); a few erect setae present near shoulder; microsculpture isodiametric, bead-like; apical microserrulations very small, almost obsolete.

Female genitalia. Sternum 8 with wide V-shaped shallow emargination in apical end; apices broadly rounded, each with a group of four short stout setae (Fig. 36a). Second gonocoxa with setae along medial margin (Fig. 36a). Second gonapophyses with medial portion 2/3 length of lateral portion (Fig. 36a). Syntergum 9 and 10 rectangular (Fig. 36b). Ventral sclerite strongly sclerotized, median ridge well developed with two finger-like brushes on inside of bursa (Figs. 36c, d, 37c-e). Membrane in place of oviduct sclerite (Figs. 36c, 37c). Spermatheca and duct *ca* 1.5 mm.

Male genitalia. Male genitalia have been described by Rivalier (1955: 84).

Geographical Variation.— Within populations, the elytral maculations, especially the middle band, vary from diffuse to almost effaced (Figs. 24a, b). A few adults with almost complete middle bands are present in São Paulo and can be confused with *C. argentata* adults.

Relationships.— *Cicindela obscurella* and *C. pretiosa* are sister species.

Habitat and Period of Activity.— Adults have been collected in December in Brazil, and in February in Argentina, Paraguay and Uruguay. Habitat unknown.

Geographical Distribution, Localities, Examined Specimens.— Inland northern Argentina, Bolivia, Paraguay and Uruguay to south Brazil (Fig. 48).

Argentina. *Salta*: San Lorenzo*, 1M, 1F, MNRJ. *Tucuman*: no locality, 1M, 2F, IOC.

Brazil. no locality, 1F, BMNH, 1F, USNM. *Minas Gerais*: Pocos de Caldas, 6F, RRMC. *Santa Catarina*: Nova Teutonia, 6!, RRMC. *São Paulo*: Campos do Jordao, 3M, 10F, MZSP.

Paraguay. Loma*, 1F, IOC; no locality, 2M, 1F, IOC, Puerto Bertoni*, 1M, 1F, IOC, Villarrica, 1M, IOC.

Uruguay. Maldonado, 1M, MNRJ; Montevideo, 4F, CASC, 1M, MNRJ, 4M, 7F, 1!, USNM; Rocha, 1M, MNRJ; Tacuarembo, 1F, MNRJ.

Cicindela (Brasiella) pretiosa Dokhtouroff
Figs. 3, 14, 25, 38, 48

Cicindela pretiosa Dokhtouroff, 1882: 276 (TYPE LOCALITY, l'Amazone). Horn, 1915: 407; 1926a, 309; 1938: 52. Blackwelder, 1944: 19. Rivalier, 1954: 263; 1955: 97.

Recognition.— The protruded central portion of the front margin of the labrum (Figs. 3a-c) together with pattern of elytral maculations distinguish adults of *C. pretiosa* from those of all other South American tiger beetles.

Synonyms and Types.— We have not seen the type specimen of *C. pretiosa*. The name is based on comparison of specimens on loan with the original description and the drawings of the elytra by Horn (1938: 52) and Rivalier (1955: 97).

Description.—

Body length. 7.0 mm M, 9.0 mm F.

Body colour. Head and pronotum slightly glossy, dark brown to black with coppery reflections; elytra dull, dark brown with coppery reflections. Venter black with blue, green, and coppery reflections.

Body setae. Pronotum with front and lateral margin moderately setose, and a few setae medially; proepisternum and mesepisternum with a few setae near ventral margin; metepisternum moderately setose throughout; metasternum and abdominal sterna setose laterally.

Other external features. Labrum edentate (or obsoletely tridentate), with front margin broadly protruding in center (Figs. 3a-c), and eight to 10 submarginal setae. Pronotum broader anteriorly (Figs. 14a-c). Coupling sulcus of mesepisternum of female a deep sinuate groove. Elytra apices slightly recurved with small apical spine; humeral lunule represented by a small subapical spot, with a small humeral spot present in some specimens, middle band short, sinuate and broad, and apical lunule reduced (Figs. 25a-c); punctation broad, shallow with green and coppery reflections; microsculpture isodiametric, bead-like.

Female genitalia. Sternum 8 with broad V-shaped posterior emargination, apices each with a group of three stout setae (Fig. 38a). Second gonocoxa with medial setae. Second gonaphophyses with medial portion 0.75 length of lateral portion (Fig. 38a). Syntergum 9 and 10 as in Figure 38b. Ventral sclerite broad, slightly sclerotized, with two apical setiferous brushes; median ridge absent. Membrane in place of oviduct sclerite (Fig. 38c). Spermatheca and duct *ca* 1.5 mm in length.

Male genitalia. Unknown.

Geographical Variation.— The pattern of the elytral maculations varies, particularly in the shape of the middle band and the presence or absence of the humeral and subhumeral spots (Figs. 25a-c).

Relationships.— *Cicindela pretiosa* and *C. obscurella* are sister species.

Habitat and Period of Activity.— Adults have been collected in January and February. Habitat unknown.

Geographical Distribution, Localities, Examined Specimens.—

Amazon Basin (Fig. 48).

Brazil. *Amazonas*: Itacoatiara (km 244), 1M, INPA; Manaus (1 km w. Taruma Falls), 1M, 1F, ICCM; Manaus (30 km. n), 1M, INPA; Manaus (60 km n.), 2M, 1F, INPA; Manaus (Reserva Ducke), 2M, 1F, INPA.

The *aureola* group

Adults of this group are characterized by bright coppery with some green on the head, pronotum and elytra, and unpigmented bell-shaped spot in abdominal sternum 5 and setae present in the bursa copulatrix of the female. The group has four species, two of which are found in Brazil, *C. amaenula* and *C. aureola*. The geographical range of the *aureola* group extends from northern Argentina northward to Venezuela. This group is a distant relative of the *argentata, hemichrysea* and *viridicollis* groups.

Cicindela (Brasiella) amaenula Chaudoir
Figs. 4, 15, 26, 39, 49

Cicindela amaenula Chaudoir , 1854: 120 (TYPE LOCALITY, les rives du fleuve des Amazones). - Horn 1906: 88; 1915: 407; 1923: 112; 1926a: 308; 1938: 52. Blackwelder, 1944: 17. - Rivalier, 1954: 263; 1955: 89. Mandl, 1963: 588, 591.

Recognition.— Specimens of *C. amaenula* are characterized by their very broad elytral maculations (Fig. 26). As Rivalier (1955: 90) observed so e *C. amaenula* specimens have narrow maculations and may be confused with *C. argentata* specimens, but the former are distinguished by their more obliquely directed middle band (Fig. 2 *cf* Fig. 23a) combined with poorly developed marginal teeth of the labrum (Fig. 4). Female genitalia (Fig. 39) and male genitalia (Rivalier, 1954: 262; 1955: 90) are also specifically distinct.

Synonyms and Types.— The name *C. amaenula* is based on comparisons of the original description with specimens on loan.

Description.—

Body length. 8.0 mm F.

Body colour. Head and pronotum slightly glossy brown to black with green and coppery reflections; elytra slightly glossy brown with coppery reflections. Venter glossy, black with coppery green and blue reflections pleura with mainly coppery and green reflections.

Body setae. Pronotum moderately setose, proepisternum sparsely setose; mesepisternum with a few setae at ventral end; metepisternum more densely setose; metasternum setose laterally; abdominal sterna 1-6 setose, more densely so on lateral margin.

Other external features. Labrum obsoletely tridentate with eight submarginal setae (Fig. 4). Posterior end of pronotum narrow (Fig. 15). Coupling sulcus of mesepisternum of female a long sinuate moderately deep groove. Apices of front trochanters with one seta. Elytra of female with slightly recurved apices, apical spine not well developed; humeral lunule reduced to shoulder and apical spots, middle band, marginal band and apical lunule well developed and broad (Figs. 26); punctation broad, shallow and with green (mainly) and coppery reflections.

Female genitalia. Sternum 8 with shallow broad V-shaped posterior emargination; apices broadly rounded each with a group of four stout setae (Fig. 39a). Second gonocoxa moderately setose near medial margin (Fig. 39a). Second gonapophyses with medial porti   0.75 length of lateral portion (Fig. 39a). Syntergum 9 and 10 as in Figure 39b. Ventral sclerite bro   pically, very narrow basally; median ridge absent. Membrane in place of oviduct sclerite (Fig. 39c). Sp   theca and duct *ca* 1.0 mm in length.

Male genitalia. Male genitalia have been described by Rivalier (1954: 262; 1955: 90).

Geographical Variation.— Even though considerable variation is evident in the pattern of the elytral maculations (Rivalier, 1955: 90) they are broad in most specimens. A geographical pattern could not be discerned as too few specimens were available for examination. Specimens examined from Matto Grosso were typically brown with coppery reflections, although a single green specimen was seen.

Relationships.— *C. amaenula* is sister to the lineage that gave rise to sister species *C. aureola* and *C. horioni* Mandl (Bolivia).

Habitat and Period of Activity.— Adults have been collected in November; they are probably riparian.

Geographical Distribution, Localities, Examined Specimens.— Inland, ranging from Matto Grosso north to the Amazon River (Fig. 49).

Bolivia. Prov. de Sara*, 1F, ICCM.

Brazil. *Amazonas*: Amazon River, 1F, BMNH, 2M, MZSP. *Goiás*: Chapada, 4M, 4F, ICCM. *Matto Grosso*: Corumba, 6M, 1F, MZSP; Cuyaba, 1M, RRMC, São Luiz de Caceres, 3M, 2F, IOC, 1M, MNRJ.

Cicindela (Brasiella) aureola Klug
Figs. 5, 16, 27, 40, 41, 49

Cicindela aureola aureola Klug, 1834: 35 (TYPE LOCALITY, sudlichen Brasilien). Horn, 1906,: 88; 1915: 407; 1926a,: 308; 1938: 52. Varas Arangua, 1925: 37. Blackwelder, 1944: 17. Rivalier, 1954: 263; 1955: 89. Vidal Sarmiento, 1966b: 34. Sumlin, 1979: 103.

Cicindela alboguttata Audouin and Brullé, 1839: 137 (not Klug) (TYPE LOCALITY, Brésil. Province de Campos-Geraes). Horn, 1896a: 353; 1915: 407; 1926a: 308. Blackwelder, 1944: 17. Vidal Sarmiento, 1966b: 34.

Cicindela argyrosticta Gemminger and Harold, 1868: 9 (replacement name for *C. alboguttata* Audouin and Brullé). Horn, 1892b: 213; 1915: 407; 1926a: 308. Blackwelder, 1944: 17. Vidal Sarmiento, 1966b: 34.

Cicindela cyanitarsis Kollar, 1836: 332 (TYPE LOCALITY, in Brasiliae provincia Ypanema). Horn, 1891: 324; 1892a: 95; 1915: 407; 1926a: 308; 1938: 52. Blackwelder, 1944: 17. Rivalier, 1955: 91. Mandl, 1960: 279; 1963: 587. Vidal Sarmiento, 1966b: 34.

Cicindela aureola jatahyana Rivalier, 1955: 91 (TYPE, a male in the MNHP general collection bearing the following label: "Jatahy État de Goyas ch. Pujol 1895-96/ Muséum Paris 1952 coll. R. Oberthür/penis 945 Rivalier/*B. aureola* s.sp. *jatahyana* mihi Rivalier det./ TYPE" (black letters on red label); TYPE LOCALITY, Jatahy (état de Goyaz)). Mandl, 1963: 587. Vidal Sarmiento, 1966b: 34.

Brasiliella aureola alverengai Mandl, 1963: 586 (TYPE LOCALITY, Jacaré P.N. Xingu, M. Grosso, Bras.).

Recognition.— The combination of edentate labrum (Figs. 5a, b), bright or dark red coppery or brown dorsum with green reflections, and reduced pattern of elytral maculations (Fig. 27) characterize *C. aureola*. Female genitalia (Figs. 40, 41) and male genitalia (Rivalier, 1954: 263; 1955: 90) also distinguish this species.

Synonyms and Types.— The names of the taxa in this complex are based on comparison of original descriptions with examined specimens and examination of the type of *C. aureola jatahyana* Rivalier. We follow Horn (1938: 52, Pl. 85) in treating *C. cyanitarsis* as a morph of *C. a. aureola* distinguished by a defined middle band. Members of *C. aureola jatahyana* Rivalier resemble the *C. cyanitarsis* form, with green punctation on the dorsum, which is the prevalent condition in *C. aureola*. *Cicindela aureola alvarengai* Mandl is a dark coppery-brown-red form of *C.*

aureola with a slender middle band.

Description.—

Body length. 8.5 mm M, 8.5-9.0 mm. F.

Body colour. Head and pronotum slightly glossy, elytra dull, almost matte. Dorsum brown with bright red-coppery (mainly) and green reflections, some specimens with dark dorsum or pronotum darker than elytra. Venter glossy with coppery, green, and blue reflections.

Body setae. Pleuron sparsely to moderately setose; mesepisternum with a few setae on ventral end only; metasternum setose laterally; abdominal sterna 1-6 setose mainly on lateral margins.

Other external features. Labrum edentate, middle portion protrudes in female with eight submarginal setae (Figs. 5a, b). Coupling sulcus of mesepisternum of female in form of sinuate groove. Apex of front trochanters each with one sensory seta, middle trochanters glabrous. Elytra with slight apical sinuation and apex recurved; apical spine small; maculations reduced, with one humeral spot, middle band, and subapical spot, or almost effaced (Fig. 27); punctures very shallow with green reflections; microsculpture isodiametric and bead-like. Pronotum as in Figure 16.

Female genitalia. Sternum 8 with wide and very shallow V-shaped posterior emargination; each apex with three very thick setae (Figs. 40a, 41a). Second gonocoxa with several setae on medial margin (Figs. 40a, 41a). Medial portion of second gonapophyses as long as or almost as long as lateral portion (Figs. 40a, 41a). Syntergum 9 and 10 as in Figures 40b, 41b. Ventral sclerite of bursa with posterior end emarginated and curved dorsally, setae present on lateral margins, median ridge absent (Figs. 40c, d, 41c, d). Membrane in place of oviduct sclerite (Figs. 40c, 41c). Length of spermatheca and duct unknown (lost in dissection).

Male genitalia. Male genitalia have been described by Rivalier (1954: 263; 1955: 90).

Geographical Variation and Subspecies.— Specimens with discontinuous or almost effaced maculations on the elytra seem to be predominant in the southern populations of Paraguay. Darker specimens appear to be more common in the populations of Matto Grosso, Brazil. Firm application of subspecific names (see Synonyms and Types section) will depend on whether these characteristics are clinal in nature or mark geographically distinct populations. Nonetheless the subspecific names *C. a. jatahyana* Rivalier and *C. a. alvarengai* Mandl are probably valid, representing populations in the northern parts of the species range and Matto Grosso respectively.

Relationships.— *Cicindela aureola* and *C. horioni* are sister species.

Habitat and Period of Activity.— Specimens have been captured in December in Matto Grosso. Habitat unknown.

Geographical Distribution, Localities, Examined Specimens.— Mainly inland, southern Brazil (Fig. 49).

Brazil. *Amazonas*: Manaus, 2F, MZSP. *Matto Grosso*: Vacaria, 5M, 3F, MZSP. *São Paulo*: São Paulo, 1F, BMNH, 1M, MZSP.

Paraguay. no locality, 1F, MZSP.

The *misella* group

Adults of this group are characterized by a broad and shallow apical emargination in abdominal sternum 8 and narrow oviduct sclerite in the female, and one or two sagittal sclerotized plates in the internal sac of the male. The group has five species, of which two are found in Brazil, *C. dolosula* and *C. misella*. The geographical range of the *misella* group extends northward from northern Argentina to Venezuela and Guatemala, and is centered in southeastern Brazil and eastern

Paraguay. The *misella* group is a distant relative of the *aureola, argentata, hemichrysea* and *viridicollis* groups.

Cicindela (Brasiella) dolosula Rivalier
Figs. 6, 17, 28, 50

Brasiella dolosula Rivalier, 1955: 95 (TYPE, a male in the MNHP general collection bearing the following labels: "1114 86" (label green on one side)/ "Salobro prov. de Bahia L. Gounelle 6.7.1885"/(extracted male genitalia)/"*B. dolosula* (type) mihi E. Rivalier det./ Muséum Paris Gounelle 1114-86/TYPE" (Black letters on red label); TYPE LOCALITY, Salobro, province de Bahia).

Recognition.— Specimens of *C. argentata* and *C. dolosula* are nearly identical except for striking differences in the internal sac of the male genitalia (female genitalia are unknown). Most specimens of *C. dolosula* are distinguished as follows: pronotum with sides feebly convex (less convex than that of *C. argentata* specimens); humeral spot almost always absent and the subhumeral spot tiny and scarcely visible; male genitalia resemble that of *C. misella* (Rivalier, 1955: 95). See also Recognition section of *C. misella*.

Description.—

Body length. 7.0 - 7.5 M, female unknown.

Body colour. Head and pronotum dull to slightly glossy with coppery tint; elytra dull, coppery brown with green punctuation; pleuron coppery-green; venter with green, blue, coppery reflections.

Body setae. Pronotum sparsely setose on lateral and front margins and a few setae on front central portions; pleuron, and lateral portions of abdominal sterna 1-6 moderately setose; mesepisternum with a few ventral setae.

Other external features. Labrum slightly projected in front, tridentate, with eight submarginal setae (this number varies from six to 10) (Fig. 6). Pronotum elongate, sides feebly convex, sutures shallow (Fig. 17). Apex of front trochanters with one sensory seta. Elytra obliquely rounded behind, slightly recurved to small apical spine. Humeral spot absent from shoulder (or almost absent), subhumeral spot very tiny, almost effaced; marginal band short, middle band and apical lunule complete; punctures large, shallow, with green reflections (Fig. 28); fine erect setae present near shoulder.

Genitalia. Female specimens have not been examined. Male genitalia have been described by Rivalier (1955: 95).

Geographical Variation.— The following notes on variation are based on observations by Rivalier (1955: 95-97). The number of submarginal setae on the labrum is mainly 8 but varies from 6-10; and the humeral spot on the shoulder of the elytra is almost always absent. No geographical pattern in the variation of these characteristics has been found.

Relationships.— *Cicindela dolosula* and *C. misella* are sister species.

Habitat and Period of Activity.— Adults have been collected in November. Habitat unknown.

Geographical Distribution, Localities, Examined Specimens.— Widespread inland, from the eastern Brazilian highlands and northern Argentina to northwestern Brazil and the Canal Zone (Fig. 50).

Argentina. *Formosa*: Guaycolec, 1F, MZSP. *Jujuy*: Dique La Dienaga, 3M, 5F, MZSP.

Brazil. *Bahia*: Salobro* (type), 1M, MNHP. *Espirito Santo*: Linhares, 3M, 3F, RRMC; Rio Itabapoana, 1M, MZSP. *Goiás*: Chapada, 2M, ICCM; Deodoro (Federal District), 1M, MZSP; Dianopolis, 6M, 3F, MZSP. *Matto Grosso*: Barra do Tapirapé, 1F, MZSP; Três Lagoas, 1M, MZSP; Xingu, 1M, MZSP. *Minas Gerais*: Unai, 1M, MZSP. *Pará*: Cachimbo, 16!, MZSP. *Roraima*: Rio Mucajai south of Boa Vista, 1M,

MZSP. *Rio de Janeiro*: Campos, 1M, RRMC; no locality, 1M, 2F, ICCM. *São Paulo*: Barueri, 2M, 1F, MZSP; Campos do Jordao, 8M, 8F, MZSP; Estrada Rio*, (km 47), 1M, 1F, MZSP; Ilha da Vitoria*, 1F, MZSP; Itu, 2M, 3F, MZSP; Nova Europa*, 1F, MZSP.

Cicindela (Brasiella) misella Chaudoir
Figs. 7, 18, 29, 42, 50

Cicindela misella misella Chaudoir, 1854: 121 (TYPE, a female in MNHP general collection bearing the following label: "Columbie/*misella* Chaud./ Muséum Paris type de Chaudoir ex collection Chaudoir/TYPE" (black letters on red label); TYPE LOCALITY, la Columbie). Bates, 1881: 14. Horn 1915: 406; 1926a: 308. Blackwelder, 1944: 17. Rivalier, 1954: 263; 1955: 93. Vidal Sarmiento, 1966b: 34. Sumlin, 1979: 104.

Cicindela misella transversalis Rivalier, 1955: 95 (TYPE, a male in the MNHP general collection bearing the following labels: "Guatemala" (green label)/ /"Muséum Paris ex. coll. M. Maindron coll. G. Babault 1930/penis 924 Rivalier/*misella m. transversalis* mihi type E. Rivalier det."; TYPE LOCALITY, Guatemala).

Recognition.— A tridentate labrum with a non-protruding front margin (Figs. 7a, b), and small humeral spot hidden from dorsal view but present on the latero-ventral side of the elytral shoulder together distinguish adults of *C. misella* from those of *C. argentata* and *C. dolosula*. Because these characteristics vary, a decisive identification can only be made on the basis of the male genitalia.

Description.—

Body length. ca 6.5 mm M and F.

Body colour. Head and pronotum slightly glossy black with green and coppery reflections, elytra dull, dark brown, pleuron and venter glossy to slightly glossy black with coppery, green, and blue reflections.

Body setae. Head glabrous. Pleuron setose, mesepisternum with a few setae near ventral end. Lateral (mainly) portions of abdominal sterna 1-6 (M,F) with appressed setae.

Other external features. Labrum narrow, tridentate, with lateral teeth broadly rounded, with basically eight (five to eight) submarginal setae (Figs. 7a, b). Pronotum narrow, broadened anteriorly (Figs. 18a, b). Coupling sulcus of mesepisternum of female with deep elongate central pit. Apex of front trochanters with one seta. Elytra with apex not recurved in males, slightly recurved in females, small apical spine (Figs. 29a, b). Pattern of elytral maculations with small humeral spot hidden on the lateroventral side of shoulder, large subhumeral spot, broadened complete middle band and apical lunule, marginal band short (Figs. 29a, b). Punctation of elytra green.

Female genitalia. Sternum 8 with shallow, very broad apical emargination, apices with four or five stout setae (Fig. 42a). Second gonocoxa and second gonapophyses as in Figure 42a. Syntergum 9 and 10 broadened apically (Fig. 42b). Ventral sclerite flat, elongate, lightly sclerotized (Fig. 42c). Oviduct sclerite narrow (Fig. 42c). Spermatheca and duct *ca* 1.0 mm long.

Male genitalia. Described and figured by Rivalier (1954: 263; 1955: 93-95) and Vidal Sarmiento (1966b: 34).

Geographical Variation.— Maculations of the elytra vary but a geographical pattern is not evident. Adults of Rivalier's *C. misella transversalis* from Guatemala have a distinct transverse middle band.

Relationships.— *Cicindela misella* and *C. dolosula* are sister species.

Habitat and Period of Activity.— Adults have been collected in March. Habitat unknown.

Geographical Distribution, Localities, Examined Specimens.— Central America and northwestern South America (probably east of the Andes) south to southwestern Brazil and Argentina (Fig. 50).

Bolivia. Chiquitos* (300 m), 4M, 1F, ICCM.
Brazil. *Matto Grosso*. Corumba, 1M, ICCM.
Colombia. Bugaba (or Buga) (800-1500'), 2M, 2F, BMNH.
Canal Zone. Barro Colorado, 1F, MZSP.

The *minarum* group

Adults of this group are characterized by a median ridge on the ventral sclerite of the bursa copulatrix of the female, and a short tooth and absence of small stiffening rib in the internal sac of the male. The group has eight species four of which are found in Brazil, *C. hamulipenis, C, brevipalpis, C. banghaasi, and C. minarum*. The geographical range of the *minarum* group extends from the Brazilian Highlands northward to Venezuela and southern Mexico. The *minarum* group is not closely related to any other group in subgenus *Brasiella*.

Cicindela (Brasiella) hamulipenis Horn
Figs. 8, 19, 30, 45, 51

Cicindela hamulipenis Horn, 1938: 14, 52, Pl. 85, Fig. 1 (HOLOTYPE, a male, in the IPZE collection bearing the following label: "Goyas/Type W. Horn/Holotypus" (black letters on red label); TYPE LOCALITY, Goyas (Brasilia center.)). - Blackwelder, 1944: 18.

Recognition.— The combination of protruding unidentate labrum with six or seven submarginal setae (Fig. 8), reduced pattern of the elytral maculations (Fig. 30), and small body size characterizes this species. The apical end of the median lobe is broad (Fig. 45a, b) and the internal sac contains sclerites with specific shapes (Fig. 45d).

Description.—

Body length. 6.0 mm M.

Body colour. Head pronotum and elytra dull, dark brown, with coppery (especially the pronotum) and green reflections. Pleuron with coppery and green reflections. Venter with green and blue-green reflections.

Body setae. Lateral margins of pronotum and pleuron moderately setose, mesepisternum of male mainly glabrous except for the ventral end. Abdominal sterna 1-6 setose, mainly on lateral margins.

Other external features. Labrum convex and elongate, unidentate, with five to seven submarginal setae (Fig. 8). Pronotum widest in anterior 0.5 (Fig. 19). Apex of front trochanters with one seta. Apices of elytra recurved to very small spine; maculations largely effaced showing remains of subapical humeral spot, middle band and apical lunule (Fig. 30); punctures of elytra shallow and green, a few larger punctures are present along median suture and on shoulder; microsculpture isodiametric and bead-like.

Female genitalia. Females were not available for examination.

Male genitalia. The median lobe is like that of other species in *Brasiella* but broader in the apical end (Figs. 45a, b); sclerites of the internal sac are specific for *C. hamulipenis*. Shield bifid apically. Stylet and arciform piece elongate, slender. Tooth slender, apex pointed. Right bar absent. Flagellum lacking (Fig. 45d).

Relationships.— *Cicindela hamulipenis* and *C. brevipalpis* are sister species.

Habitat and Period of Activity.— Adults have been collected in January. Habitat unknown.

Geographical Distribution, Localities, Examined Specimens.— Only the Holotype (IPZE) and one other male were examined. Both specimens were collected

in Goiás, the non-Holotype in Dianopolis, 11-14.1.1962 (Fig. 51).
Brazil. *Goiás*: Dianopolis, 1M, MZSP; no locality, 1M IPZE.

Cicindela (Brasiella) brevipalpis Horn
Figs. 9, 20, 31, 46, 51

Cicindela brevipalpis Horn, 1926b: 77 (TYPE LOCALITY, Vacarias von Sud-Matto Grosso); 1926a: 308:
1938: 52. Blackwelder, 1944: 17.

Recognition.— The character state of small body size, *ca* 6.0 mm long, elytra that lack both a distinct shoulder at the anterior end and maculations (Fig. 31), and an indistinct 5-dentate labrum and 6 submarginal setae (Fig. 9) taken together are diagnostic for adults of *C. brevipalpis*.

Synonyms and Types.— The name *C. brevipalpis* Horn is based on comparison of the original description with a male specimen on loan from IPZE labelled: "Matto Grosso Vacaria XII-22/Type W. Horn/Syntypes" (black letters on a red label).

Description.—
Body length. ca 6.0 mm M.
Body colour. Body dull, black, with some coppery and green reflections on the head, thorax and elytra.
Body setae. Pronotum with a few setae on lateral margins and central disc. Pleuron and lateral portions of the metasternum with appressed setae, only the ventral end of the mesepisternum setose; abdominal sterna 3-6 inclusive sparsely setose.
Other external features. Head with protruding eyes. Labrum indistinctly five dentate, six submarginal setae, with the middle four close to the margin (Fig. 9). Pronotum narrow, broader at the anterior end (Fig. 20). Tibia rufotestaceous. Apex of front trochanters with one sensory seta, middle trochanters glabrous. Elytra lacking distinct shoulder, apices not recurved, apical spine well developed; maculations absent; punctures very shallow and marked with green (mainly) and coppery spots (Fig. 31); microsculpture isodiametric, bead-like. Flight wings absent.
Female genitalia. Females were not available for dissection.
Male genitalia. Apex of median loabe with short protruding tip; not hooked. Internal sac with at least one apical setal brush. Flagellum lacking. Sclerites of internal sac very well sclerotized; the shield bears two sharp apices, arciform piece long and strongly oblique, stylet obliquely truncated at apex, tooth of moderate size and very thin in the apical 0.5 (Figs. 46a-c).

Relationships.— *Cicindela brevipalpis* and *C. hamulipenis* are sister species.

Habitat and Period of Activity.— The syntypes were found running quickly between grass in sparse grasslands in December 1922 (Horn, 1926b: 78).

Geographical Distribution, Localities, Examined Specimens.— The syntypes, collected in Vacaria, Matto Grosso (Fig. 51), are the only known specimens.
Brazil. *Matto Grosso*: Vacaria, 1M, IPZE.

Cicindela (Brasiella) banghaasi Horn
Figs. 10, 21, 32, 43, 51

Cicindela banghaasi Horn, 1907: 24 (TYPE LOCALITY, Cuyaba, Matto-Grosso); 1915: 408; 1923: 112;
1926a: 310; 1938: 53. Blackwelder, 1944: 17. Rivalier, 1954: 263; 1955: 98.

Recognition.— The character state combination of the sparsely setose frons and gena, unidentate labrum with 8 setae, pattern of elytral maculations with a broad oblique middle band (Fig. 32), round pit-like coupling sulcus of the mesepisternum

of the female, and structure of female genitalia (Figs. 43a-c) distinguishes *C. banghaasi* from other Brazilian species of *Cicindela*. Also structures of the internal sac of the male are specific (Rivalier, 1955:98).

Synonyms and Types.— The name *C. banghaasi* is based upon comparison of the original description with six syntypes, one female and five males, on loan from the IPZE, each labelled as follows: "Staudinger Cuyaba Matt. Gr./ Type! Dr. W. Horn/Syntypes"; and with one large group label "*Cicindela Banghaasi* H.6".

Description.—

Body length. 6.5-7.0 mm M, 7.5 mm F.

Body colour. Dorsum dull; head and pronotum black or very dark brown with some coppery and green reflections; elytra very dark brown with coppery reflections and large green puncture spots. Pleuron coppery (mainly), blue and green. Venter black with blue-green (mainly) and some coppery reflections.

Body setae. Head with a few setae between the eyes, on the frons, clypeus in some specimens, and genae. Pronotum and pleuron moderately setose. All abdominal sterna setose, more densely so laterally.

Other external features. Labrum unidentate to tridentate (indistinct) with eight submarginal setae (Fig. 10). Pronotum broader anteriorly (Fig. 21). Coupling sulcus of mesepisternum of female a deep round pit. Apex of front trochanters with one sensory seta. Elytra with recurved apex to very small spine; humeral spot and subhumeral spot small, marginal band and apical lunule broad, middle band broad and oblique; punctation green, with a row of much larger green umbilicate punctures along with the median sutures, and some intermediate in size clustered near the shoulder (Fig. 32); a few erect setae present near shoulder; apical microserrulations very small.

Female genitalia. Sternum 8 with wide V-shaped emargination in apical end, apices each with three stout setae and two smaller setae (Fig. 43a). Second gonocoxa with a few setae near apical end of medial margin; and second gonapophyses as shown in Figure 43a. Syntergum 9 and 10 as shown in Figure 43b. Ventral sclerite with a round darkened basal end and central broad median ridge well developed (Fig. 43c). Membrane in place of oviduct sclerite (Fig. 43c). Spermatheca and duct (broken in dissection), short, approximately 1.0 mm.

Male genitalia. Male genitalia have been described by Rivalier (1955: 98).

Relationships.— *C. banghaasi* is sister to the lineage that gave rise to sister species *C. hamulipenis* and *C. brevipalpis*.

Habitat and period of activity.— Unknown.

Geographical Distribution, Localities, Examined Specimens.—

Cuyaba, Matto Grosso (Fig. 51).

Brazil. *Matto Grosso*: Cuyaba, 1F, 5M, IPZE, 1F, RRMC.

Cicindela (Brasiella) minarum Putzeys
Figs. 11, 22, 33, 44, 51

Cicindela minarum Putzeys, 1845: 369 (TYPE LOCALITY, Brésil. Province des Mines.). Horn, 1915: 406; 1926a: 307; 1938: 52. Blackwelder, 1944: 18. Rivalier, 1954: 263; 1955: 92,98,99.

Recognition.— The character combination of the short unidentate labrum with 7-12 submarginal setae (Figs. 11a, b), oblique truncation of the apical end of the elytra and colour pattern of elytral maculations (Figs. 33a, b) distinguishes *C. minarum* from other species of *Cicindela*.

Description.—

Body length. ca 8.0 mm M, *ca* 8.5 mm F.

Body colour. Dorsum dull, black with copper and green reflections. Pleuron copper (mainly) and some green. Venter black with mainly blue and purple reflections.

Body setae. Pronotum with a few setae along lateral margin and middle suture. Proepisternum and mesepisternum with a few sparse setae mainly in ventral 0.5; other pleural sclerites, the lateral 0.5 of the metasternum and abdominal sterna 1-6, moderately setose.

Other external features. Labrum short and unidentate, almost tridentate, with seven (M) to 12 (F) submarginal setae (Figs. 11a, b). Pronotum square-shaped with parallel sides. Coupling sulcus of mesepisternum of female a deep groove with a pit in the center. Apex of front trochanters with one seta. Apical end of elytra obliquely truncated and recurved to small apical spine (Figs. 33a, b). Pattern of elytral maculations reduced with subapical spot present or absent, marginal band short, discontinuous sinuate middle band, and complete apical lunule with recurved hook-shape at distal end (Figs. 33a, b). Punctation large, shallow, blue and green, and sparsely distributed. Microsculpture isodiametric, bead-like.

Female genitalia. Sternum 8 with broad V-shaped apical emargination, apices each with a group of three stout setae (Fig. 44a). Second gonocoxa with several setae on medial margin (Fig. 44a). Gonapophyses short, stout (Fig. 44a). Syntergum 9 and 10 as in Figure 44b. Ventral sclerite darkly sclerotized; median ridge well developed (Fig. 44c). Membrane in place of oviduct sclerite (Fig. 44c). Spermatheca and duct length unknown (broken in dissection).

Male genitalia. Male genitalia have been described by Rivalier (1955: 99).

Relationships.— *Cicindela minarum* is sister to the lineage that gave rise to *C. nebulosa* Bates (Nicaragua to Colombia and Ecuador) and sister species *C. mandli* Brouerius van Nidek (Chiapas, Mexico) and *C. insularis* Brouerius van Nidek (Trinidad).

Habitat and Period of Activity.— Specimens of *C. minarum* have been collected in December and April. Habitat unknown.

Geographical Distribution, Localities, Examined Specimens.– Geographical distrubution mainly inland in southern Brazil (Fig. 51).

Brazil. *Espirito Santo*: no locality, 1F, IOC, 1M, MZSP. *Matto Grosso*: Vacaria, 1   2F, MZSP. *Minas Gerais*: Mar de Espanha*, 1M, 1F, IOC, 1M, 1F, MZSP, 1F, RRMC; Passa Quatro, 1M, 1F, IOC.

Subgenus *Gaymara* new subgenus

Type species.— *Cicindela chlorosticta* Kollar, 1836: 332 (here selected).

Derivation of name.— From first given names of Gayla E. Freitag, Gavin W. Freitag, Margot E. Freitag and Barbara L. Barnes (junior author), who have assisted the senior author in studies on tiger beetles.

Recognition.— Adults of this subgenus are distinguished by the five characters given in couplet 4 of the key. In addition the head is mainly glabrous, with elongate tridentate labrum; elytral maculations are partially reduced; the apex of the median lobe of the male consists of a short ventral hook (straight in *C. anulipes*), and a flagellum is absent from the internal sac; the spermatheca and duct together are approximately 1.0 - 2.0 mm long. (See the Recognition section of subgenus *Brasiella* for similarities between it and the subgenus *Gaymara*.

Species groups.— This subgenus has two groups, the *chlorosticta* group and *anulipes* group, that together include five species. Both groups are found in eastern South America mainly in southeastern Brazil.

Geographical distribution.— The range of this subgenus extends from northern Argentina northward to southern parts of the Ama n basin.
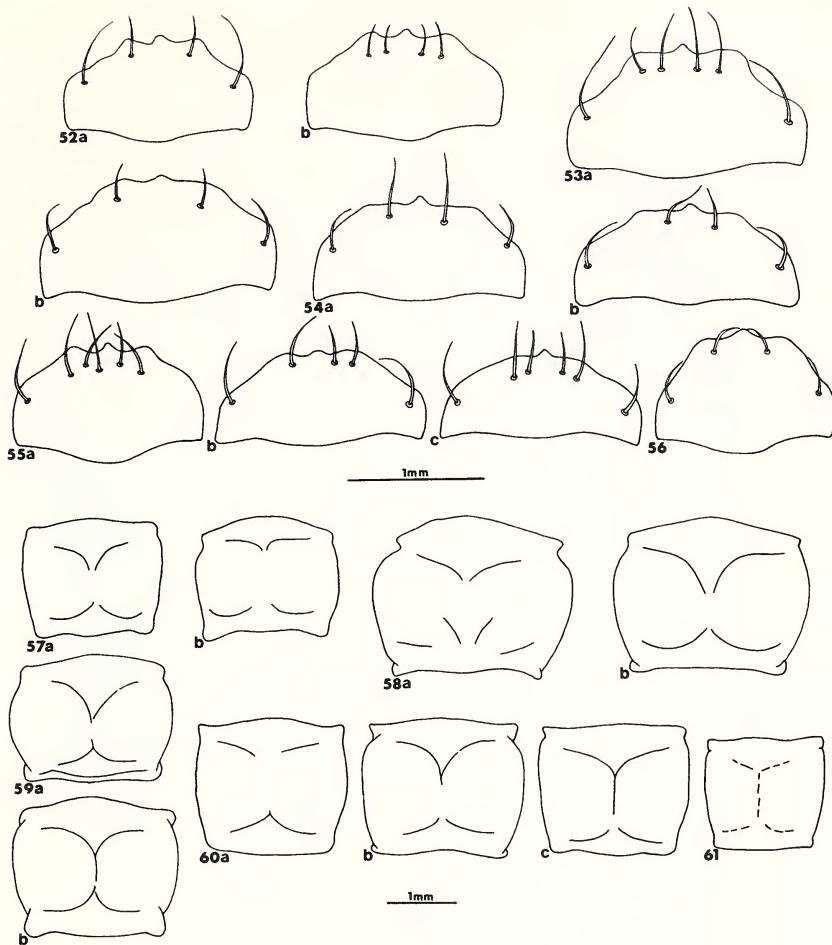
Figs. 52–56. Labrum, dorsal aspect. 52, *Cicindela chlorosticta* Kollar: (a) female, Esperanca do Sul, S.P.; (b) male, Jatai, Go.; 53, *C. staudingeria* Horn: (a) female, Jatai, Go.; (b) male, Vacaria, M. Grosso; 54, *C. nigroreticulata* Horn, Ronda Alta, R.G. do Sul: (a) female; (b) male; 55, *C. paranigroreticulata* n.sp., Tramandai, R.G. do Sul: (a), (b) female; (c) male; 56, *C. anulipes* Horn, female, Utiariti, Rio Papagaio, M. Grosso. Figs. 57–61. Pronotum, dorsal aspect. 57, *Cicindela chlorosticta* Kollar: (a) female; (b) male; 58, *C. staudingeria* Horn: (a) female; (b) male; 59, *C. nigroreticulata* Horn: (a) female; (b) male; 60, *C. paranigroreticulata* Horn n. sp.: (a), (b) female; (c) male; 61, *C. anulipes* Horn, female.
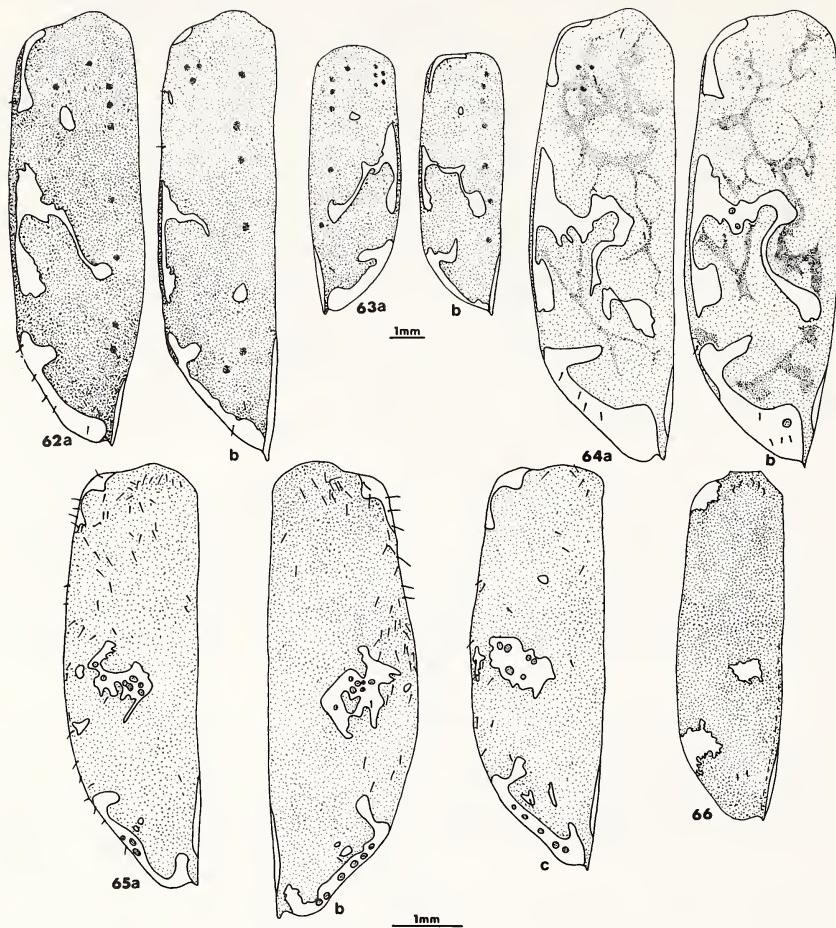
Figs. 62–66. Elytron, dorsal aspect. 62, *Cicindela chlorosticta* Kollar: (a) female; (b) male; 63, *C. staudingeria* Horn: (a) female; (b) male; 64, *C. nigroreticulata* Horn: (a) female; (b) male; 65, *C. paranigroreticulata* n. sp.: (a), (b) female; (c) male; 66, *C. anulipes* Horn, female.
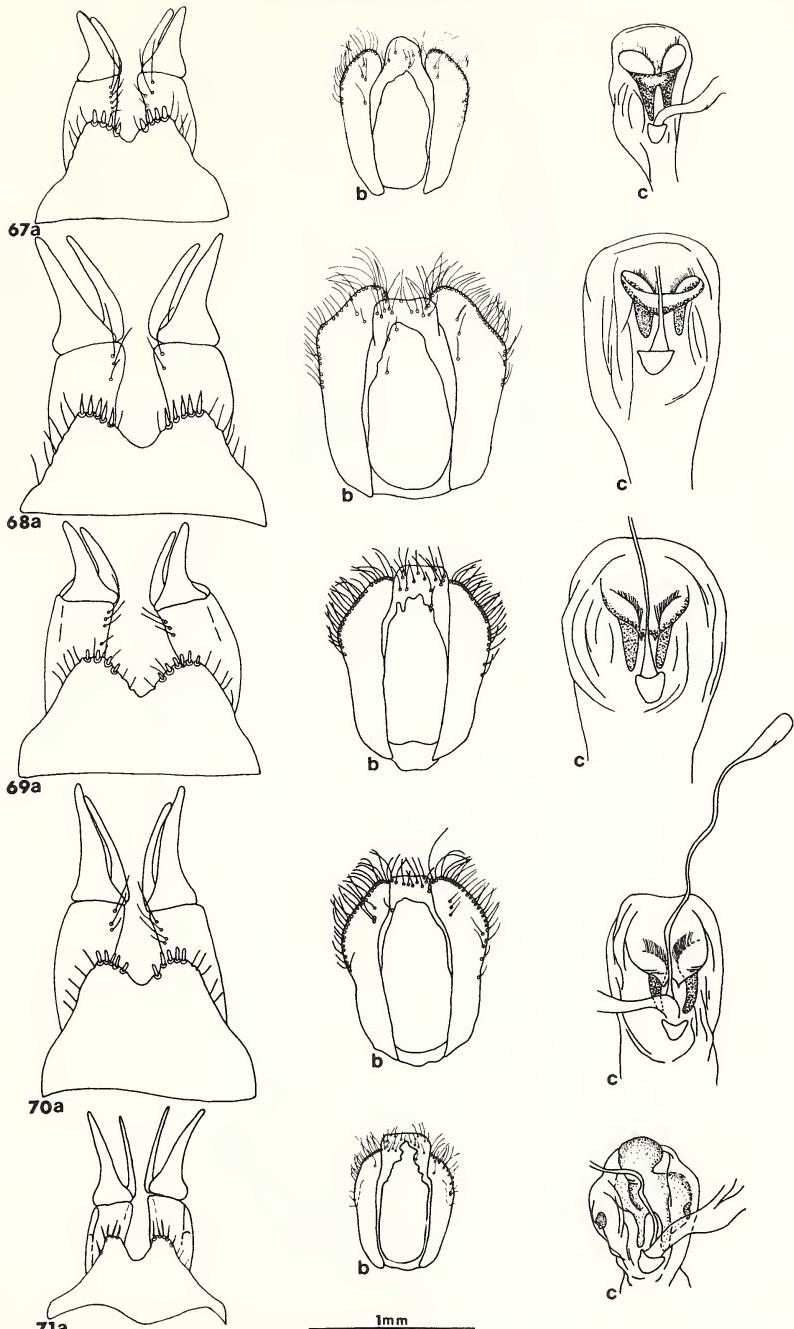
Figs. 67–71. Female genitalia: (a) sternum 8, second gonocoxa, second gonapophyses, ventral aspect; (b) syntergum 9&10, dorsal aspect; (c) bursa copulatrix, oviduct sclerite, oviduct, spermatheca and duct, ventral sclerite, ventral aspect. 67, *Cicindela chlorosticta* Kollar; 68, *C. staudingeria* Horn; 69, *C. nigroreticulata* Horn; 70, *C. paranigroreticulata* n. sp.; 71, *C. anulipes* Horn.
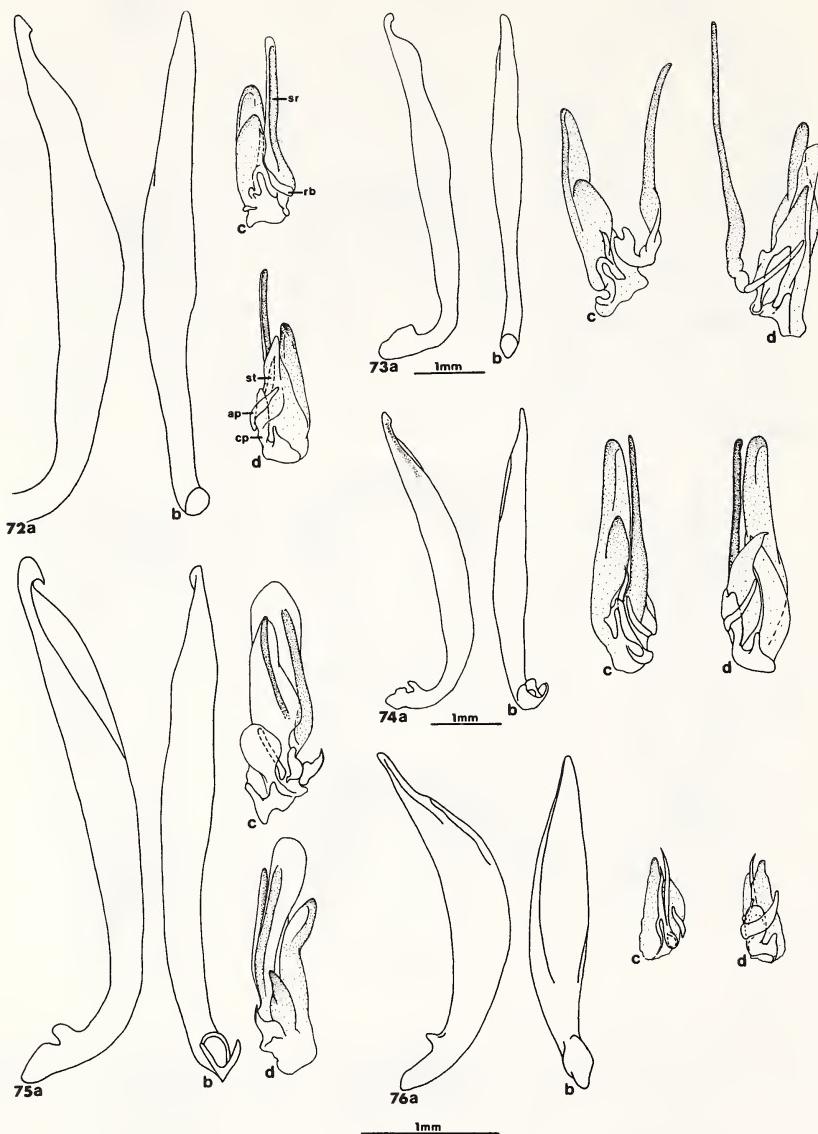
Figs. 72–76. Male genitalia: median lobe (a) right lateral aspect; (b) dorsal aspect; (c) internal sac, arciform piece (*ap*), central plate (*cp*), right bar (*rb*), spiny rod (*sr*), stylet (*st*), right lateral aspect; (d) left lateral aspect. 72, *Cicindela chlorosticta* Kollar; 73, *C. staudingeria* Horn; 74, *C. nigroreticulata* Horn; 75, *C. paranigroreticulata* n. sp.; 76, *C. anulipes* Horn. Localities for Figures 57–76 as for 52–56.

Fig. 77. Map showing the geographical distribution of the species *Cicindela chlorosticta* Kollar (●); *C. staudingeria* Horn (■) *C. nigroreticulata* Horn (▲); *C. paranigroreticulata* n. sp. (♦); *C. anulipes* Horn (✦). Open squares and open circle with a cross represent state records for *C. staudingeria* Horn and *C. anulipes* Horn respectively.

Phylogenetic relationships.— Subgenus *Gaymara* is sister to the lineage that gave rise to *Plectographa* and *Cylindera*.

The *chlorosticta* group

Adults of this group are characterized by two swirls of rugosity between eyes, broad pronotum, and large elytral foveae. The group has four species all of which are found in Brazil, *C. chlorosticta, C. staudingeria, C, nigroreticulata,* and *C. paranigroreticulata.* The geographical range of the *chlorosticta* group extends from southeastern Brazil into southern parts of the Amazon basin. The *chlorosticta* and *anulipes* groups are sister groups.

Cicindela (Gaymara) chlorosticta Kollar
Figs. 52, 57, 62, 67, 72, 77

Cicindela chlorosticta Kollar, 1836: 332 (TYPE LOCALITY, in Brasiliae provincia Ypanema). Horn, 1915: 404; 1926a: 306; 1938: 52. Blackwelder, 1944: 17. Rivalier, 1954: 264; 1955: 99. Vidal Sarmiento, 1966a: 257; 1966b: 35. Sumlin, 1979: 105.
Cicindela chlorosticta smaragdina Horn, 1893: 198 (TYPE LOCALITY, São Paulo); 1915: 404; 1926a: 306. Blackwelder, 1944: 17.

Recognition.— Adults of the sister species of *C. chlorosticta* and *C. staudingeria* are distinguished from other Brazilian tiger beetles by a deeply rugose head and pronotum, bright coppery dorsum and pleuron, and pattern of elytral maculations, in particular the oblique middle band, and row of large foveae along the median suture of elytra (Figs. 62, 63). Adults of *C. chlorosticta* are distinguished from those of *C. staudingeria* by the smaller body size; a relatively narrow pronotum (Fig. 57 *cf.* Fig. 58); four setae on apex of each lobe of sternum 8 (Fig. 67a *cf.* Fig. 68a); very elongate pair of posterior extension of the ventral sclerite of the bursa copulatrix and narrow oviduct sclerite (Fig. 67c *cf.* Fig. 68c) in the female; and relatively shorter tooth (spiny field) and stylet (spiny rod) of the internal sac of the male (Figs. 72c, d *cf.* Figs. 73c, d).

Synonyms and Types.— Adults of *C. smaragdina* are blue or green members of *C. chlorosticta* found in São Paulo. We follow Horn, 1926a: 404 in treating *C. smaragdina* as a synonym of *C. chlorosticta*. These colour morphs appear to be rare.

Description.—

Body length. 8.0-8.5 mm M, *ca* 8.5 mm F.

Body colour. Head and pronotum deeply rugose, bright coppery and with some green. Elytra matte light brown or coppery, combined with a little green in some specimens. A few adults with blue or green dorsum. Pleuron glossy and bright coppery. Venter mainly coppery with some green, purple and blue; center of abdomen black with mainly purple reflections.

Body setae. Head glabrous. Pleuron sparsely to moderately setose. Lateral portions of abdominal sterna 1-5 (F) and 1-6 (M) with appressed setae.

Other external features. Vertex of head with two wide shallow pits (swirls of rugosity) between hind margins of eyes. Labrum elongate tridentate, with four to six submarginal setae (Figs. 52a, b), Pronotum broadened anteriorly, sides not protruding (Figs. 57a, b). Coupling sulcus of mesepisternum of female a

long, moderately deep groove. Apex of front trochanters with one seta. Elytra with apex slightly recurved to a well developed spine in females (Figs. 62a, b). Pattern of elytral maculations with discontinuous humeral lunule and oblique complete or discontinuous middle band (Figs. 62a, b). Punctation of elytra green; with a row of foveate punctures along median suture and a cluster near shoulder (Figs. 62a, b).

Female genitalia. Sternum 8 with shallow and broad apical emargination, apices broadly rounded, each apex with four stout setae (Fig. 67a). Second gonocoxa with four or five setae in medial margin (Fig. 67a). Second gonapophyses short (Fig. 67a). Syntergum 9 and 10 as in Figure 67b. Ventral sclerite with two elongate posterior projections; row of fine setae on anterior margins (Fig. 67c). Oviduct sclerite narrow (Fig. 67c). Spermatheca and duct probably short (broken in dissection).

Male genitalia. Apical end of median lobe narrowly tapered (Figs. 72a, b). Internal sac without flagellum. Large tooth in the form of an elongate spiny field consisting of two lobes. Stylet joined to base of tooth short with pointed apex. Spiny rod extended beyond apical end of tooth. Arciform piece moderately broad. Central plate large (Figs. 72c, d).

Geographical Variation.— The dorsal colour and pattern of elytral maculations vary slightly but a geographical pattern is not evident.

Relationships.— *Cicindela chlorosticta* and *C. staudingeria* are sister species.

Habitat and Period of Activity.— Adults have been collected from October to March. Habitat unknown.

Geographical Distribution, Localities, Examined Specimens.— Central and southeastern Brazil to northeastern Argentina and Paraguay (Fig. 77).

Brazil. *Goiás*: Chapada, 2M, ICCM; Jatai, 2M, IOC, 3M, MZSP; Rio Verde, 1M, IOC. *Matto Grosso*: Utiariti, 1M, MZSP; Vacaria, 2M, 2F, MZSP. *São Paulo*: Avanhand (Garbe L.)*, 4M, 6F, MZSP; Eng. Coelho*, 1M, 1F, IOC; Esperanca do Sul*, 1M, 1F, MZSP; Guatapara*, 1M, 2F, MZSP; Onda Verde*, 1F, MZSP; Piraju, 1M, 1F, MZSP.

Paraguay. Caaguazu, 1M, 1F, MNRJ.

Cicindela (Gaymara) staudingeria Horn
Figs. 53, 58, 63, 68, 73, 77

Cicindela staudingeri Horn, 1892c: 368 (not Kraatz) (TYPE LOCALITY, São Paulo); 1915: 404; 1926a: 306. Blackwelder, 1944: 17. Sumlin 1979: 105.
Cicindela staudingeria Horn, (replacement name for *Cicindela staudingeri* Horn), 1915: 404; 1926a: 306; 1938: 52. Blackwelder, 1944: 17. Rivalier, 1954: 264; 1955: 99. Sumlin, 1979: 105

Recognition.— Adults of *C. staudingeria* are distinguished from other Brazilian tiger beetles by character combination of the large body size. *ca* 10.0-12.0 mm long, markedly rugose head and pronotum, two wide fairly deep pits between the hind margins of the eyes, bright coppery reflections from the dorsum and pleuron, particularly from the proepisternum, and pattern of elytral maculations (Figs. 63a, b). See also Recognition section for *C. chlorosticta*.

Synonyms and Types.— The name *C. staudingeria* is based upon comparison of the original description of *C. staudingeri* Horn with four males and one female in the IPZE, each labelled as: "Staudinger, São Paulo/Type ! Coll. W. Horn/Syntypus *Cicindela staudingeri* Horn 5".

Description.—
Body length. 10.0-11.0 mm M, 12.0 mm F.
Body colour. Head and pronotum deeply rugose, bright coppery and some green; elytra matte light brown and coppery and faintly green in some specimens. Pleuron glossy and bright coppery. Venter mainly

coppery with some green, blue and purple reflections; center of abdomen black with some blue, green or purple.

Body setae. Pleuron sparsely setose. Lateral margins of abdominal sterna 1-5 (F) and 1-6 (M) covered with appressed setae.

Other external features. Vertex of head of most adults with two wide shallow pits between hind margins of eyes. Labrum elongate, tridentate, weakly so in some specimens, with four to seven (most commonly six) submarginal setae (Figs. 53a, b). Pronotum broad, sides ampliate, in most specimens sutures moderately deep (Figs. 58a, b). Coupling sulcus of mesepisternum of female a long and moderately deep groove. Apex of front trochanters with one sensory seta. Elytra with apex slightly recurved to a well developed spine (Figs. 63a, b). Pattern of elytral maculations with discontinuous to almost effaced humeral lunule, middle band oblique, marginal band and apical lunule complete (Figs. 63a, b). Punctation green. Large foveate punctures along median suture and a cluster of smaller ones near middle of shoulder (Figs. 63a, b).

Female genitalia. Sternum 8 with shallow and broadly rounded V-shaped apical emargination, each apex with five stout fairly long setae (Fig. 68a). Second gonocoxa with several setae in medial margin (Fig. 68a). Second gonapophyses elongate (Fig. 68a). Syntergum 9 and 10 as in Figure 68b. Ventral sclerite with two posterior projections, recurved apex and row of fine setae on apical end (Fig. 68c). Oviduct sclerite short and broad (Fig. 68c). Spermatheca and duct probably short (broken in dissection).

Male genitalia. Apical end of median lobe narrowly tapered (Figs. 73a, b). Internal sac without flagellum. Very long bilobed spiny field in place of the large tooth. Stylet joined to base of tooth, short, apex sharp, bent. Slender spiny rod extended far beyond apical end of tooth. Arciform piece long; central plate large. Right bar wide (Figs. 73c, d).

Geographical Variation.— Dorsal colour, pattern of elytral maculations, and number of submarginal setae of the labrum vary within populations, though geographical patterns of variation are not apparent.

Relationships.— *Cicindela staudingeria* and *C. chlorosticta* are s ter species.

Habitat and Period of Activity.— Adults have been collected f om October to March. Habitat unknown.

Geographical Distribution, Localities, Examined Specimens.— Southeastern Brazil to northern Argentina and Uruguay (Fig. 77).

Brazil. *Goiás*: Chapada, 6M, 5F, ICCM: Jatai, 1F, IOC,1F, MZSP. *Matto Grosso*:Murtinho*, 1M, IOC; no locality, 2M, 3F, MZSP. *São Paulo*: Batatais, 1M, IOC; no locality, 1M, IOC, 1M, 1F, MZSP.

Uruguay. Rivera, 2M, MNRJ; Tacuarembo, 1F, MNRJ.

Cicindela (Gaymara) nigroreticulata Horn
Figs. 54, 59, 64, 69, 74, 77

Cicindela nigroreticulata Horn, 1927: 139 (TYPE, a female in IPZE bearing the following label: "Cochilha Grande R. Grande d. Sul/Type W. Horn/ Holotypus (black letters on red label)/*nigroreticulata*"; TYPE LOCALITY, Cochilha Grande, Rio Grande do Sul); 1938: 52. Blackwelder, 1944: 19.

Recognition.— Adults of *C. nigroreticulata* are distinguished from those of other Brazilian species by the colouration of the elytra and pattern of elytral maculations. Many dark brown lines form a reticulated pattern against the lighter brown and coppery ground colour, and the middle band is strongly curved (Figs. 64a, b). In addition, the labrum is unidentate or weakly tridentate with 4 submarginal setae (Figs. 54a, b), and a pair of wide pits are located between the hind margins of the eyes.

Description.—
Body length. 9.0 mm M, *ca* 9.0-9.5 mm F.

Body colour. Dorsum of head and pronotum slightly glossy, with bright coppery and green reflections; elytra dull brown coppery or green, with a reticulated pattern formed by many dark brown lines (Figs. 64a, b). Venter glossy, with green and coppery reflections.

Body setae. Pleuron, lateral portions of abdominal sterna with sparsely to moderately dense appressed setae, most of the mesepisternum glabrous.

Other external features. Vertex of head and pronotum deeply rugose. Two wide pits located on vertex between hind margins of eyes. Tooth of mentum elongate. Labrum unidentate or weakly tridentate, four submarginal setae (Figs. 54a, b). Pronotum broad, sides ampliate, sutures deep (Figs. 59a, b). Coupling sulcus of mesepisternum of female a groove with center depressed. Legs red-coppery throughout. Apex of front trochanters with one seta. Elytra tapered apically, apex recurved to short apical spine. Maculations of elytra separate and clearly defined; humeral lunule short not reaching central disc, middle band strongly curved (Figs. 64a, b); punctation almost effaced, large shallow punctures near shoulders and anterior portions of disc beside median suture.

Female genitalia. Sternum 8 with shallow V-shaped posterior emargination; apices broadly rounded each with four to six short thick setae (Fig. 69a). Second gonocoxa with a few setae on median edge (Fig. 69a). Second gonapophyses short and broad at base (Fig. 69a). Syntergum 9 and 10 broadened posteriorly (Fig. 69b). Ventral sclerite bulbous, with two elongate posterior projections, row of fine setae on anterior dorsal margin (Fig. 69c). Oviduct sclerite shield-like, well sclerotized (Fig. 69c). Spermatheca and duct elongate (broken in dissection), greater than 1.5 mm in length.

Male genitalia. Apical end of median lobe slender, apex with sharp ventral emargination (Figs. 74a, b). Internal sac without flagellum. Stylet short sinuate, apex sharp, joined to base of tooth. Elongate unsclerotized spiny field-like bilobed tooth and thin rod each of equal length. Two basal membranous lobes present. Arciform piece slender; central plate large. Right bar narrow, elongate (Figs. 74c, d).

Geographical Variation.— The pattern of reticulations on the elytra varies appreciably within and among populations.

Relationships.— *Cicindela nigroreticulata* and *C. paranigroreticulata* are sister species.

Habitat and Period of Activity.— Adults have been collected in February. Habitat unknown.

Geographical Distribution, Localities, Examined Specimens.— Inland Rio Grande do Sul, Brazil (Fig. 77).

Brazil. *Rio Grande do Sul*: Cochilha Grande, 1F (holotype), IPZE; Ronda Alta*, 1M, 2F, MNRJ; Santo Augusto*, 2M, 1F, ICCM.

Cicindela (Gaymara) paranigroreticulata new species
Figs. 55, 60, 65, 70, 75, 77

Type Specimens.— HOLOTYPE, a female in the collection of MNRJ labelled: "Brasil Rio Gde. do Sul Tramandai 14-11-64 C.S. Carbonell A. Mesa y M.A. Monné/Holotype *Cicindela paranigroreticulata* R. Freitag, B.L. Barnes" (red label). PARATYPES, one male and one female in the MNRJ labelled same as Holotype, but type label is: "Paratype *Cicindela paranigroreticulata* R. Freitag and B.L. Barnes" (blue label). TYPE LOCALITY, Tramandai Rio Gde do Sul.

Recognition.— The character state combination of black body, large body size, 8.0-9.0 mm long, extensive head and body pubescence, setose elytra, and pattern of elytral maculations (Figs. 65a-c) distinguish adults of *Cicindela paranigroreticulata* from those of other Brazilian species of *Cicindela*.

Description.— *Body length.* 8.0 mm M, *ca* 9.0 mm F.

Body colour. Head, pronotum, pleuron and venter slightly glossy; elytra dull. Body black with obscure green and coppery reflections on the elytra and pleuron. Four basal articles of the antenna coppery and green; articles 5-11 moderate pale rufopiceous. Legs with coppery and green reflections.

Body setae. Vertex, frons, clypeus and genae with scattered setae, and a tuft of setae on the front inner margins of each eye. Pronotum setose, except for central disc. Elytra sparsely setose mainly on basal 0.5, medial along suture and lateral margins. Pleuron, lateral portion of metasternum, and later portions of abdominal sterna moderately setose. Dorsal 0.5 of mesepisternum glabrous.

Other external features. Vertex of head deeply rugose. Two obsolete wide pits (swirls of rugosity) on vertex between hind margins of eyes. First antennal article with one long apical seta and one short medial seta. Tooth of mentum elongate. Labrum elongate tridentate; six to eight submarginal setae (Figs. 55a-c). Pronotum broad expanded in apical 0.5 (Figs. 60a-c). Coupling sulcus of mesepisternum of female an elongate groove with deep middle. Procoxa, mesocoxa and lateral portion of metacoxa moderately setose. Apex of front trochanters with one seta. Femora, tibia, and tarsi moderately setose. Apex of elytra recurved to small spine; maculations of elytra reduced, humeral lunule short, middle band discontinuous not reaching lateral margin of elytra, apical lunule elongate (Figs. 65a-c). Elytral punctations shallow marked by green and coppery metallic spots; a row of larger punctures near median suture and another short row inside the shoulder; microsculpture mainly isodiametric. Apices of elytra with microserrulations.

Female genitalia. Sternum 8 with shallow U-shaped posterior emargination; apices broadly rounded each with five short thick setae (Fig. 70a). Second gonocoxa with a few setae on medial edge (Fig. 70a). Second gonapophyses elongate (Fig. 70a). Syntergum 9 and 10 broadened posteriorly (Fig. 70b). Ventral sclerite wide, lightly sclerotized, two elongate posterior projects slightly curved medially, row of fine setae on dorsal anterior margin (Fig. 70c). Oviduct sclerite lightly sclerotized, almost transparent, shield-shaped with lateral flanges (Fig. 70c). Length of spermatheca and duct *ca* 2.0 mm.

Male genitalia. Apical end of median lobe slender, apex sharply hooked posteriorly (Figs. 75a, b). Internal sac was accidentally everted. Flagellum absent. Stylet joined to base of tooth very short, stout with pointed apex. Spiny field-like bilobed tooth and two rod-like extensions of equal length. Arciform piece slender; central plate large. Right bar was not seen (Figs. 75c, d).

Relationships.— *Cicindela paranigroreticulata* and *C. nigroreticulata* are sister species.

Habitat and Period of Activity.— Type collected on or beside ocean shore, February or November, 1964.

Geographical Distribution, Localities, Examined Specimens.— Known only from Tramandai, Rio Grande do Sul, Brazil (Fig. 77).

Brazil. *Rio Grande do Sul*: Tramandai, 1F (holotype), 1M, 1F, (paratypes), MNRJ.

The *anulipes* group

Adults of this group are characterized by some or all setae of labrum positioned very near the anterior margin, and long mentum tooth. The group has only one species, *C. anulipes*, which is found in southeastern Brazil and the Brazilian Highlands. This group and the *chlorosticta* group are sister groups.

Cicindela (Gaymara) anulipes Horn
Figs. 56, 61, 66, 71, 76, 77

Cicindela anulipes Horn, 1897a: 255 (TYPE, a male in the IPZE bearing the following labels: "Staudinger, Minas Geraes/Type !, Dr. W. Horn/ Holotypus" (black letters on red label) "*Cicindela anulipes* Horn"; TYPE LOCALITY, Minas Geraes); 1915: 405; 1923: 112; 1926a: 307; 1938: 58. Blackwelder, 1944: 16. Rivalier, 1954: 264; 1955: 99.

Recognition.— The character state combination of the elongate and weakly tridentate labrum, deep and evenly distributed punctures of the proepisternum, pattern of the elytral maculations reduced in extent (Fig. 66), sclerotized oviduct sclerite and shape of ventral sclerite of the bursa copulatrix distinguishes *C. anulipes* from other species of *Cicindela* in Brazil. The internal sac of the male contains a unique bifid stylet (Fig. 76c).

Synonyms and Types.— The name is based upon examination of the type specimen and other specimens on loan.

Description.—

Body length. 7.0-7.5 mm M, 7.5 mm F.

Body colour. Dorsum dull, black; elytra matte and slightly velvety. Venter and pleuron balck with green, coppery and blue reflections; legs with testaceous sections.

Body setae. Margins of pronotum, proepisternum, mesepisternum and lateral margins of abdominal sterna 1-6 with appressed setae. Elytra with a few erect setae near shoulder.

Other external features. Tooth of mentum long. Labrum elongate, convex, slightly tridentate; four submarginal setae (Fig. 56). Pronotum narrowed at posterior end, sutures shallow (Fig. 61). Punctures of proepisternum deep and evenly distributed. Coupling sulcus of mesepisternum of female a broad and moderately deep groove. Apex of front trochanters each with one seta. Elytra with apical end tapered and slightly recurved to a small spine (Fig. 66). Pattern of elytral maculations with humeral spot on shoulder, middle spot on disc, and marginal spot near the apex (Fig. 66). A small portion of the marginal band may or may not be present. Punctures of elytra large gradually becoming deeper near shoulder. Elytra with a few erect setae near shoulder.

Female genitalia. Sternum 8 with deep and narrow emargination in apical end, apices each acutely rounded, and with 5 thick setae (Fig. 71a). Second gonapophyses elongate, narrow, median portion almost as long as lateral portion (Fig. 71a). Syntergum 9 and 10 as in Figure 71b. Ventral sclerite with wide apical end spatulate and deflected dorsally (Fig. 71c); two elongate posterior projections (Fig. 71c). Oviduct sclerite short (Fig. 71c). Spermatheca and ducts *ca* 1.0 mm long.

Male genitalia. Apical end of median lobe slender, apex not hooked (Figs. 76a, b). Internal sac without flagellum. Stylet unique bifid, joined to base of tooth, elongate. Tooth spiny field with long stylet-like piece. Arciform piece very wide; central plate large; right bar present (Figs. 76c, d).

Geographical Variation.— Patterns of geographical variation in examined adult characteristics were not apparent. Some adults had a marginal spot on the elytra.

Relationships.— *Cicindela anulipes* is sister to the lineage that gave rise to sister species *C. chlorosticta* and *C. staudingeria*, and sister species *C. nigroreticulata* and *C. paranigroreticulata*.

Habitat and Period of Activity.— Unknown.

Geographical Distribution, Localities, Examined Specimens.— Goiás, Matto Grosso, Minas Gerais, and Rio Grande do Sul (Fig. 77).

Brazil. *Goiás*: Chapada, 2M, 5F, ICCM; Jatai, 1F, IOC, 3M, 11F, MZSP; Jolaby*, 1F, MZSP. *Matto Grosso*: Utiariti, 9M, 10F, MZSP. *Minas Gerais*: no locality, 1M, IPZE, 1F, MZSP. *Rio Grande do Sul*: Tramandai, 3M, 2F, MNRJ.

Subgenus *Plectographa* Rivalier

Subgenus *Plectographa* Rivalier, 1954: 265 (TYPE SPECIES, *Cicindela gormazi* Reed, by original designation).

Recognition.— Adults of this subgenus are distinguished by the four characters given in couplet 5 of the key. In addition the labrum is basically unidentate with 4-11 submarginal setae; apical end of the median lobe is tapered and not hooked; in
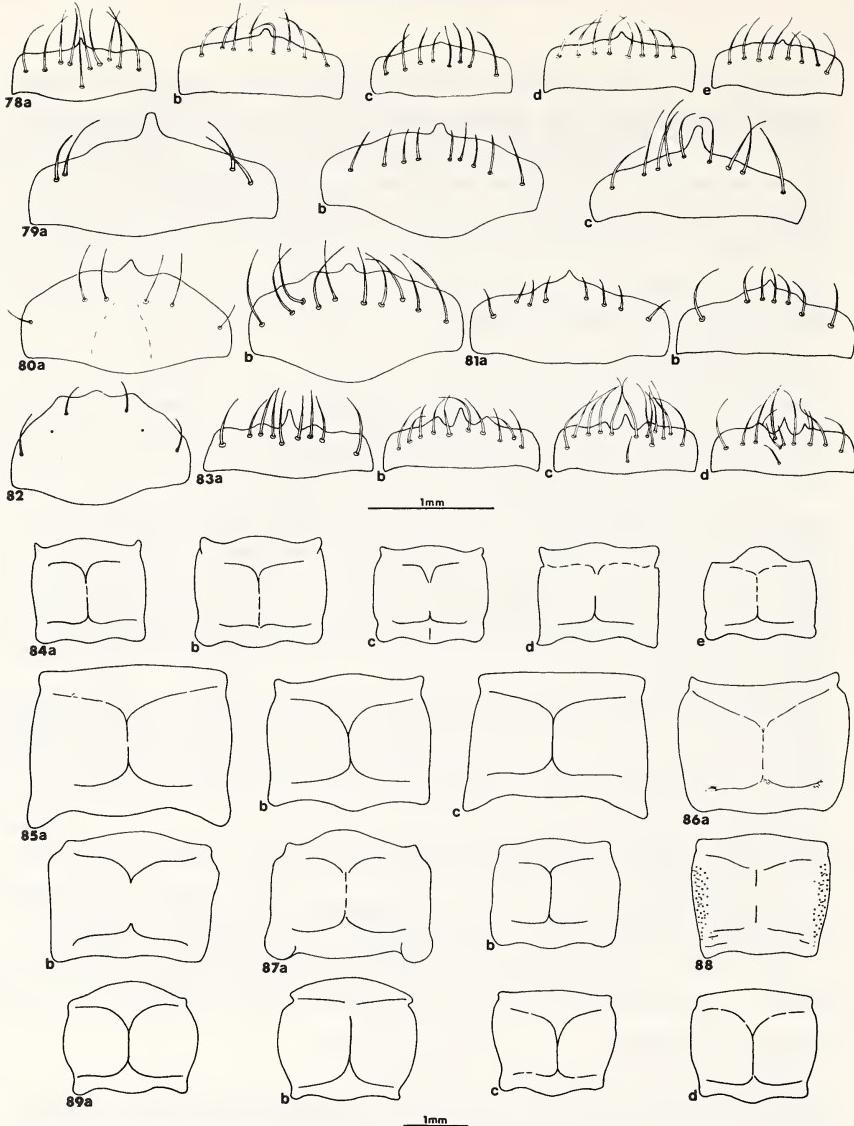
Figs. 78–83. Labrum, dorsal aspect. 78, *Cicindela suturalis* Fabricius: (a) female, Maturaca, Am.; (b) female, (c) male, Russas, Ce.; (d) female, (e) male, São Luis; Mar.; 79, *C. nivea* Kirby: (a) female, (b) male, Florianopolis, Sta. Cat.; (c) female, Vacaria, M. Grosso; 80, *C. melaleuca* Dejean: (a) female, Rio Grande do Sul; (b) female, Buenos Ayres, B.A.; 81, *C. patagonica* Brullé: (a) *C. p. cherubim* Chevrolat, female, Montevideo, Uruguay; (b) *C. p. bergiana* Horn, male, Rio Grande do Sul; 82, *C. nigrovittata* Horn, female, Minas Gerais; 83, *C. apiata* Dejean: *C. a. apiata*, (a) female, (b) male, Rio de Janiero, R.d.J.; *C. a. claussenii* Putzeys, (c) female, (d) male, Rio Grande do Sul. Figs. 84–89. Pronotum, dorsal aspect. 84, *Cicindela suturalis* Fabricius: (a) female, Maturaca, Am.; (b) female, (c) male, Russas, Ce.; (d) female, (e) male, São Luis, Mar.; 85, *C. nivea* Kirby: (a) female, (b) male, Florianopolis, Sta. Cat.; (c) female, Vacaria, M. Grosso; 86, *C. melaleuca* Dejean: (a) female, Rio Grande do Sul; (b) female, Buenos Ayres, B.A.; 87, *C. patagonica* Brullé: (a) *C. p. cherubim* Chevrolat, female, Montevideo, Uruguay; (b) *C. p. bergiana* Horn, male, Rio Grande do Sul; 88, *C. nigrovittata* Horn, female, Minas Gerais; 89, *C. apiata* Dejean: *C. a. apiata* (a) female, (b) male, Rio de Janeiro, R.d.J.; *C. a. claussenii* Putzeys, (c) female, (d) male, Rio Grande do Sul.
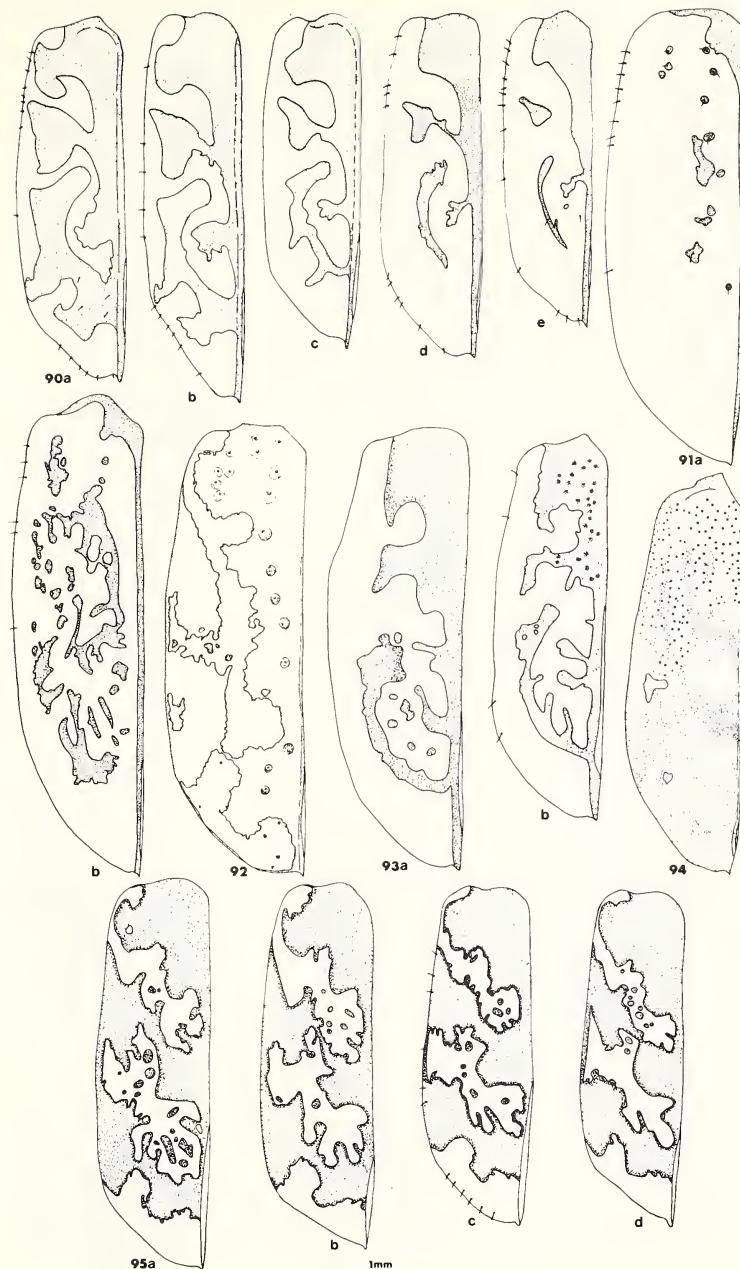
Figs. 90–95. Elytron, dorsal aspect. 90, *Cicindela suturalis* Fabricius: (a) female, Maturaca, Am.; (b) female, (c) male, Russas, Ce.; (d) female, (e) male, São Luis, Mar.; 91, *C. nivea* Kirby: (a) male, Florianopolis, Sta. Cat.; (b) female, Vacaria, M. Grosso; 92, *C. melaleuca* Dejean, female, Rio Grande do Sul; 93, *C. patagonica* Brullé: (a) *C. p. cherubim* Chevrolat, female, Montevideo, Uruguay; (b) *C. p. bergiana* Horn, male, Rio Grande do Sul; 94, *C. nigrovittata* Horn, female, Minas Gerais; 95, *C. apiata* Dejean: *C. a. apiata* (a) female, (b) male, Rio de Janeiro, R.d.J.; *C. a. claussenii* Putzeys, (c) female, (d) male, Rio Grande do Sul.
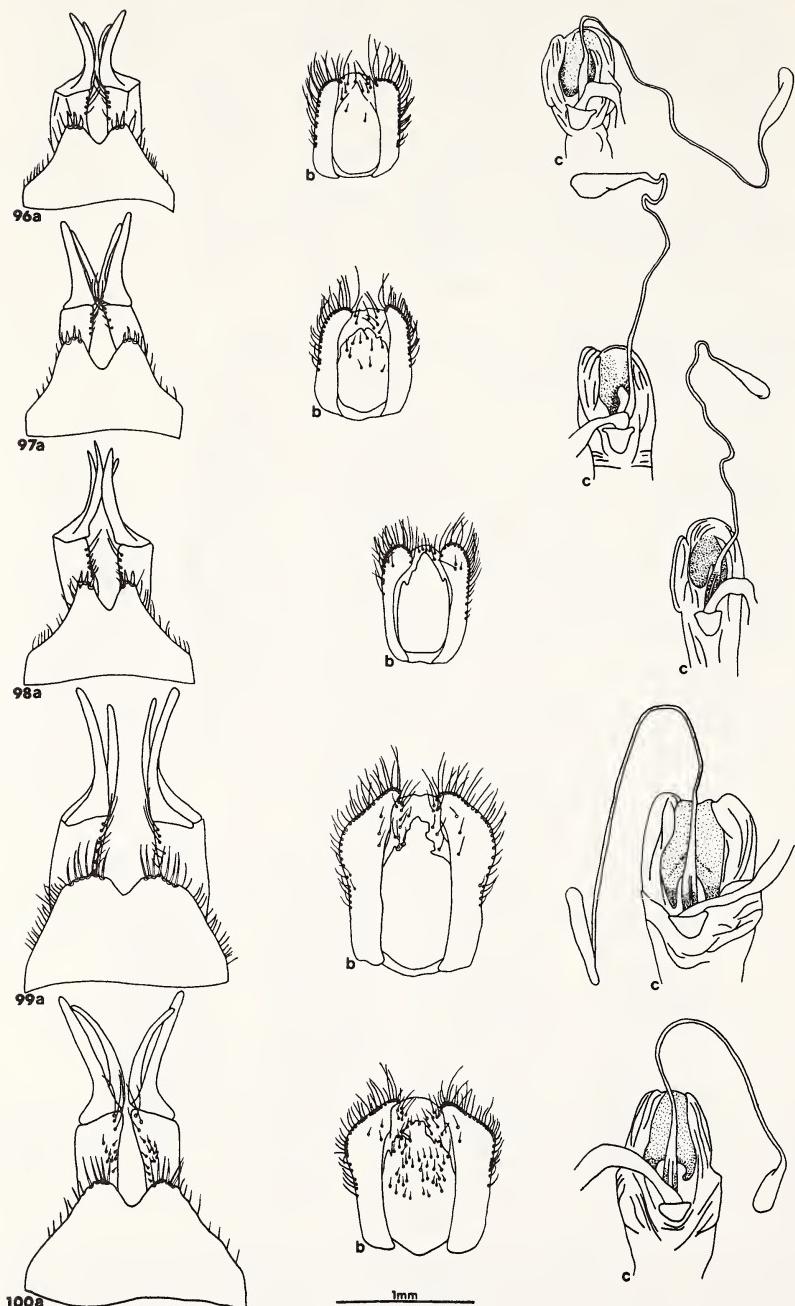
Figs. 96–100. Female genitalia: (a) sternum 8, second gonocoxa, second gonapophyses, ventral aspect; (b) syntergum, 9 & 10, dorsal aspect; (c) bursa copulatrix, oviduct sclerite, oviduct, spermatheca and duct, ventral sclerite, ventral aspect. *Cicindela suturalis* Fabricius: 96, Maturaca, Am.; 97, Russas, Ce.; 98, São Luis, Mar.; *C. nivea* Kirby: 99, Florianopolis, Sta. Cat.; 100, Vacaria, M. Grosso.
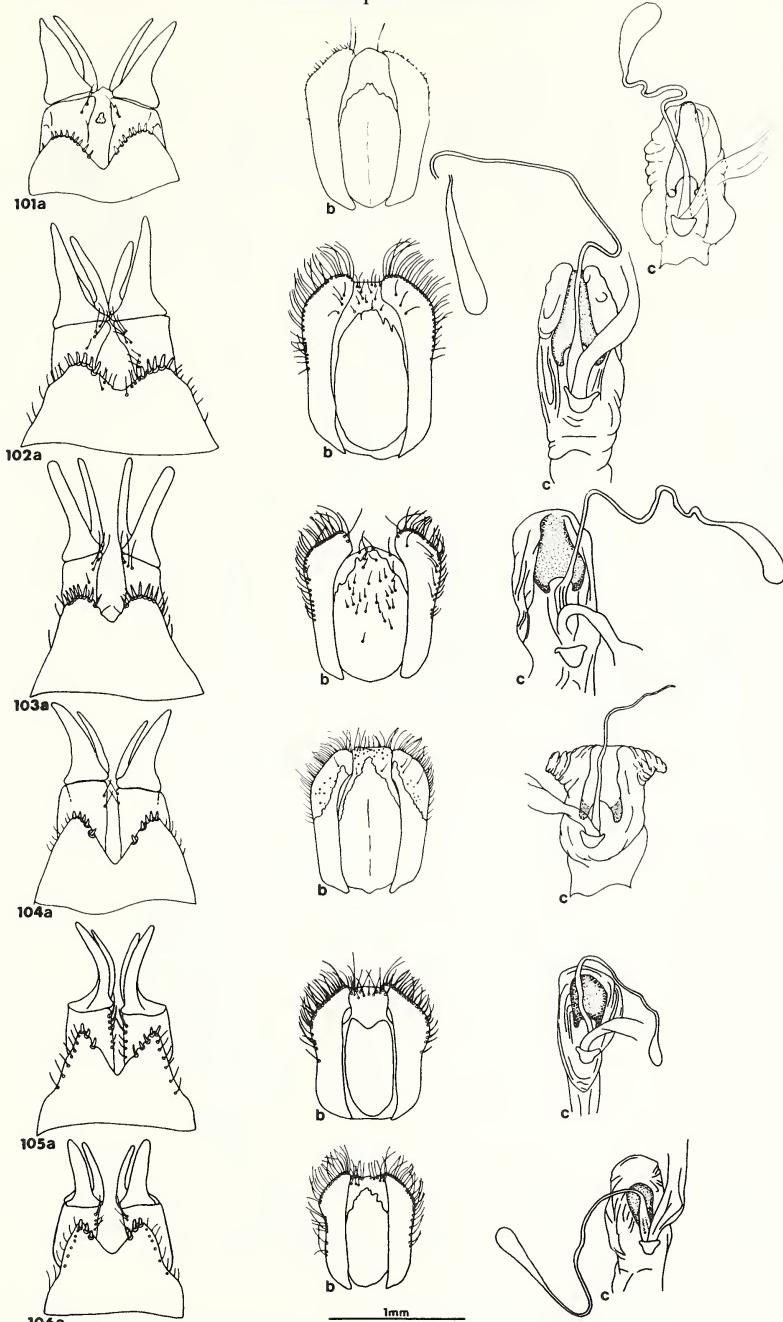
Figs. 101–106. Female genitalia: (a) sternum 8, second gonocoxa, second gonapophyses, ventral aspect; (b) syntergum, 9 & 10, dorsal aspect; (c) bursa copulatrix, oviduct sclerite, oviduct, spermatheca and duct, ventral sclerite, ventral aspect. *C. melaleuca* Dejean: 101, Rio Grande do Sul; 102, Buenos Ayres, B.A.; 103, *C. patagonica cherubim* Chevrolat, Montevideo, Uruguay; 104, *C. nigrovittata* Horn, Minas Gerais; 105, *C. apiata apiata* Dejean, Rio de Janeiro, R.d.J.; 106, *C. a. claussenii* Putzeys, Rio Grande do Sul.
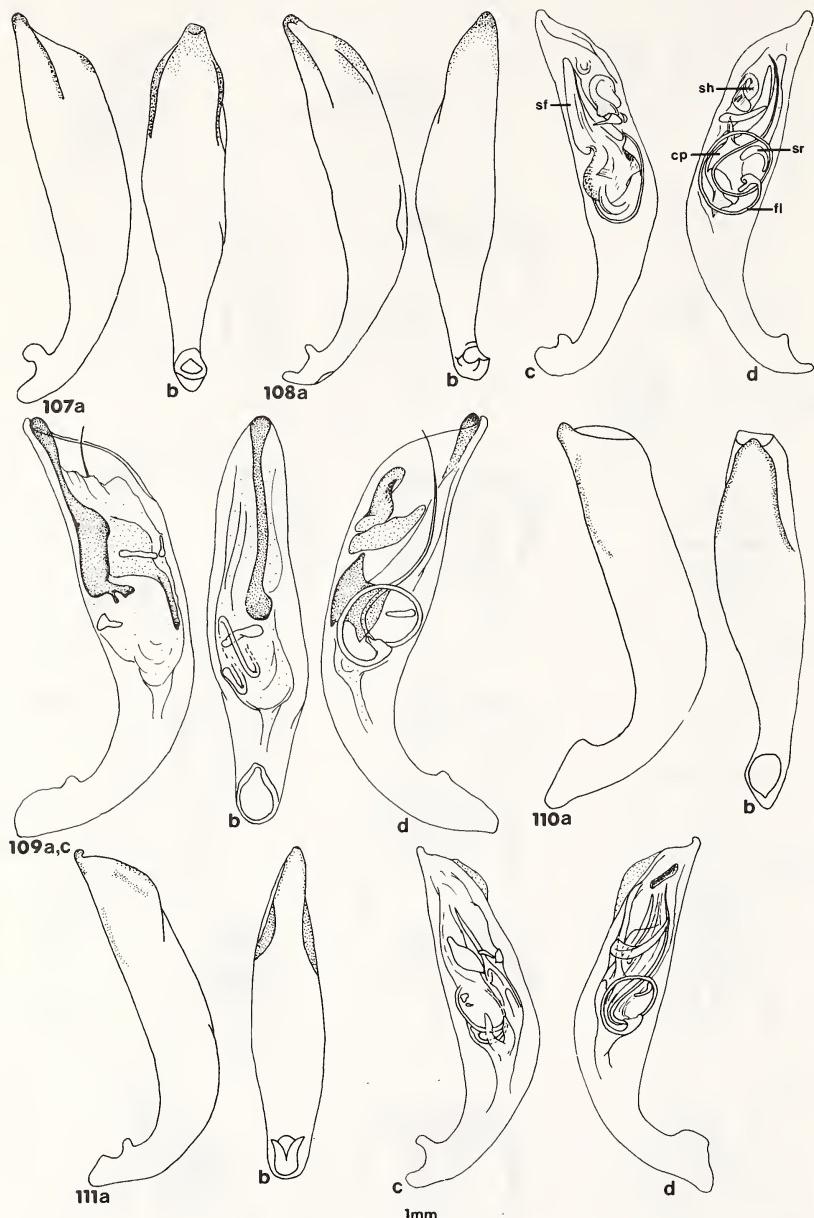
Figs. 107–111. Male genitalia: median lobe (a) right lateral aspect, (b) dorsal aspect; (c) internal sac, arciform piece, central plate (*cp*), flagellum (*fl*), right bar, shield (*sh*), spatulate field (*sf*), small stiffening rib (*sr*), stylet, tooth, right lateral aspect; (d) left lateral aspect. *Cicindela suturalis* Fabricius: 107, Russas, Ce.; 108, São Luis, Mar.; 109, *C. nigrovittata* Horn, Minas Gerais; 1 . *C. apiata apiata* Dejean, Rio de Janiero, R.d.J.; 111, *C. a. claussenii* Putzeys, Rio Grande do Sul.

Fig. 112. Map showing the geographical distribution of the species *Cicindela suturalis* Fabricius (●), *C. nivea nivea* Kirby (■), and *C. n. orbignyi* Guérin-Méneville (▲). Open circles represent state records, and those with an adjacent point indicate records taken from the literature for *C. suturalis* Fabricius.

Fig. 113. Map showing the geographical distribution of the species *Cicindela melaleuca* Dejean (●), and *C. patagonica* Brullé (■).

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Fig. 114. Map showing the geographical distribution of the species *Cicindela nigrovittata* Horn (♦), *C. apiata apiata* Dejean (●), and *C. a. claussenii* Putzeys (■). Open circles are state or country records for *C. apiata apiata* Dejean taken from the literature.

females the ventral sclerite of the bursa copulatrix is glabrous and has two elongate posterior projections; the spermatheca and duct together are approximately 2.5 - 4.5 mm long.

Species groups.— This subgenus has five species groups that include 18 species. Four groups, *suturalis* group, *melaleuca* group, *nigrovittata* group, and *apiata* group, are found in Brazil.

Geographical distribution.— The geographical range of this subgenus extends from temperate Chile and Patagonia northward to the West Indies, and is centered in northern Argentina.

Phylogenetic relationships.— *Plectographa* and *Cylindera* are sister subgenera.

The *suturalis* group

Adults of this group are characterized by bright coppery and some green body colouration. The group has seven species, two of which, *C. suturalis* and *C. nivea* are found in Brazil. The geographical range of the *suturalis* group extends from central Chile and Patagonia northward to the West Indies, and is centered in northern Argentina. The *suturalis* and *melaleuca* groups are sister groups.

Cicindela (Plectographa) suturalis Fabricius
Figs. 78, 84, 90, 96, 97, 98, 107, 108, 112

Cicindela suturalis Fabricius, 1798: 62 (TYPE LOCALITY, in America St. Thomas); 1801: 242.–Herbst, 1806: 207.–Dejean, 1825: 129. –Horn, 1915: 403; 1926a: 305; 1938: 52.–Leng and Mutchler, 1916: 693.–Blackwelder, 1944: 20.–Jonge Poerink, 1953: 133. –Rivalier, 1954: 266.–Balazuc and Chalumeau, 1978: 22-25.–Ivie, 1983: 195.

Cicindela trifasciata Dejean, 1825: 85(not Fabricius) (TYPE LOCALITY, Cayenne).–Horn, 1915: 403; 1926a: 306.–Blackwelder, 1944: 20.

Cicindela hebraea Klug, 1834: 20 (TYPE LOCALITY, Cayenne).–Putzeys, 1874: 117.–Horn, 1915: 403; 1926a: 306; 1938: 52. –Leng and Mutchler, 1916: 694.–Varas Arangua, 1930: 154.–Blackwelder, 1944: 20.–Jonge Poerink, 1953: 135. –Rivalier, 1954: 266.–Mandl, 1963: 578.–Balazuc and Chalumeau, 1978: 25.

Cicindela hieroglyphica Klug, 1834: 30 (TYPE LOCALITY, Pará in Brasilien).–Horn, 1915: 403; 1926a: 306.–Blackwelder, 1944: 20.

Cicindela chlorocephala Mannerheim, 1837: 17 (TYPE LOCALITY, in insula Porto Rico).–Horn, 1915: 403; 1926a: 306.–Blackwelder, 1944: 20.

Cicindela insidiosa Gistl, 1837: 48 (TYPE LOCALITY, in America septentrionali, in Antillis).–Horn, 1915: 403; 1926a: 306.

Cicindela nocturna Steinheil, 1875: 96 (TYPE LOCALITY, Magdalenae fluminis, Colombia).–Horn, 1915: 403; 1926a: 306; 1938: 52.– Leng and Mutchler, 1916: 694. –Blackwelder, 1944: 20.–Jonge Poerink, 1953: 137-138.–Rivalier, 1954: 266.–Mandl, 1958: 26.–Balazuc and Chalumeau, 1978: 26.

Cicindela hebraea guadeloupensis Fleutiaux and Sallé, 1889: 358 (TYPE LOCALITY, Guadeloupe).–Horn, 1915: 403; 1926a: 306.–Leng and Mutchler, 1916: 694. –Blackwelder, 1944: 20.–Jonge Poerink, 1953: 137.–Balazuc and Chalumeau, 1978: 25.

Cicindela suturalis helvaea Horn, 1903: 333 (not Klug) (TYPE LOCALITY, Ciudad Bolivar, Venezuela).

Cicindela trifasciata boliviana Mandl, 1956: 386 (TYPE LOCALITY, Santa Cruz); 1958; 26; 1964: 16. NEW SYNONYMY.

Recognition.— Narrow to broad distinctive elytral maculations (Figs. 90a-e) and a unidentate labrum bearing 8-10 submarginal setae (Figs. 78a-e) distinguish specimens of this species.

Synonyms and Types.— Names were based upon comparison of original descriptions with specimens on loan.

Description.—

Body length. 6.5-8.0 mm M, 6.5-9.0 mm F.

Body colour. Head, pronotum and elytra slightly glossy with coppery, green, and less frequently blue, reflections. Pleuron and venter mainly coppery, and green.

Body setae. Dense appressed setae on lateral portions of pronotum, pleuron, ventral 0.33 of mesepisternum, and abdominal sterna 1-6.

Other external features. Labrum unidentate with eight to 10 (more frequently eight) submarginal setae (Figs. 78a-e). Pronotum with parallel sides, sutures moderately deep (Figs. 84a-e). Coupling sulcus of mesepisternum of female a deep sinuate groove. Apex of front trochanters with a single sensory seta. Elytra with long apical spine, (longer in *C. hebraea* form specimens); maculations complete and joined together, broadened in *C. suturalis* form specimens); punctations generally deep, subsutural row of large punctures absent (Figs. 90a-e); microsculpture isodiametric; apical serrulations present.

Female genitalia. Sternum 8 with deep V-shaped apical emargination, apices each with three (less frequently two) medium length setae (Figs. 96a-98a); second gonocoxa with a few long and short setae along medial margin (Figs. 96a-98a); second gonapophyses as in Figures 96a-98a; syntergum 9 and 10 as in Figures 96b-98b; bursa with right lateral extension; ventral sclerite lightly sclerotized with posterior lateral extensions, median ridge absent (Figs. 96c-98c) oviduct sclerite with well developed lateral extensions (Figs. 96c-98c); length of spermatheca and duct 3.00-3.25mm.

Male genitalia. Median lobe with short blunt apex (Figs. 107a, b-108a, b). Internal sac with flagellum 1.5 loops at base. Stylet present next to tooth, the large spatulate apex of tooth characteristic of *Plectographa* forms not elongate. Arciform piece, right bar, central plate, shield and small stiffening rib all well developed (Figs. 107c, d-108c, d).

Geographical Variation and Subspecies.— Populations composed of specimens with narrow to broad but well defined elytral maculations are widespread in Brazil. At least one identified specimen with continuous pale maculations (*C. suturalis* form) has been collected near Manaus. In most specimens the maculations are broad (*C. hebraea* form). They may be continuous in part (Figs. 90d, e) or the lunules may be clearly discernible (Figs. 90a-c). Specimens with narrow elytral maculations (*C. nocturna, C. guadeloupensis* or *C. boliviana* forms) are less frequent. The form of the elytral maculations seems to be variable in local populations, and geographical patterns are not evident. In addition the female genitalia tend to be uniform within and among populations (Figs. 96-98).

Morphologically distinct geographical populations, in Brazil at least, apparently do not occur, and consequently we have not applied subspecific names. A varied elytral pattern and other discordant characteristics predominate in populations of *C. suturalis* in South America north of Brazil and the West Indies. A thorough revision is required as regional studies of this species (complex) have not led to taxonomic stability (Leng and Mutchler, 1916: 693-695; Jonge Poerink, 1953: 133-138; Mandl, 1958: 24-28; Balazuc and Chalumeau, 1978: 23).

Relationships.— *Cicindela suturalis* and *C. sinuosa* Brullé (n. Argentina, Paraguay and Uruguay) are sister species.

Habitat and Period of Activity.— Specimens have been collected on sea beaches and on extensive sand beaches along rivers (Pearson, 1984) during February, May, June, September and December.

Geographical Distribution, Localities, Examined Specimens.— Islands of the Caribbean from Jamaica and Hispaniola south to Trinidad, northern half of South America south to southeastern Brazil (Fig. 112).

Bolivia. Cochabamba, 1F, MZSP.

Brazil. *Amazonas*: Arima (near Rio Purus), 1F, ICCM, Barcelos, 1M, MZSP; Manaus, 1M, INPA, 1M, MZSP; Manaus (Ilha de Marchantaria), 2M, 1F, INPA; Maturaca (Alto Rio Cauaburi), 1F, MZSP; Nova Olinda, 7F, ICCM; Tapuruquara, 1F, MZSP. *Bahia*: Canavieiras, 1M, IOC; Encruzilhada (980m), 1M, RRMC; Joazeiro, 1F, ICCM; Rio São Francisco*, 2F, IOC; Villa Nova*, 2M, MZSP. *Ceará*: Aracaty, 1F, MZSP; Barreiras*, 1M, MZSP; Ceará Beach *, 5M, 2F, ICCM; Russas, 1M, 1F, MZSP. *Espirito Santo*: 1F, MZSP. *Maranhao*: no locality, 2M, 4F, ICCM; São Luis, 4M, 6F, MZSP. *Matto Grosso*: Pimentel*, 1M, 2F, MZSP; S. Domingos, 1M, MZSP; Sinop*, 1F, RRMC. *Pará*: Belem, 1M, MZSP; Cachimbo, !, IOC; Morroda*, 1F, ICCM; no locality, 1F, ICCM, Santarem, 2M, 2F, ICCM. *Paraíba*: Coremas, 1M, 2F, MZSP. *Santa Catarina*: Imbituba, 1M, MNRJ.

Peru. Chancayo*, 2M, MNRJ.

Cicindela (Plectographa) nivea Kirby
Figs. 79, 85, 91, 100, 112

Cicindela nivea nivea Kirby, 1818: 376 (TYPE LOCALITY, in Brasilia).– Dejean, 1825: 128.–Horn, 1915: 409; 1926a: 311; 1938: 53. –Fernandez, 1936: 109.–Blackwelder, 1944: 19.–Rivalier, 1954: 266.–Mandl, 1963: 578.–Vidal Sarmiento, 1966b: 41.–Sumlin, 1979: 115.

Cicindela conspersa Dejean, 1825: 127 (TYPE LOCALITY, l'île de Sainte-Catherine, au Brésil).–Brullé, 1837: 9. –Horn, 1915: 409; 1926a: 311; 1938: 53.–Barattini, 1929: 1221.–Fernandez, 1936: 109.–Blackwelder, 1944: 19.–Vidal Sarmiento, 1966b: 43.

Cicindela niver orbignyi Guérin-Ménéville, 1839: 296 (TYPES, a male and female in the MNHP general collection bearing the following labels: "intricata" (green label, on male pin only)/Muséum Paris Patagonie (Patagones) d'Orbigny 1834/ 34 6073" (on a folded round label green on one side)/"TYPE" (black letters on red label); TYPE LOCALITY, la Patagonie). –Horn, 1915: 409; 1926a: 311; 1938: 53.–Fernandez, 1936: 109.–Blackwelder, 1944: 19. Rivalier, 1954: 266.–Vidal Sarmiento, 1966b: 43.–Sumlin, 1979:115.

Cicindela intricata Brullé, 1837: 7 (TYPE LOCALITY, l'Ile aux Cachons, dans la baie de San-Blas (Patagonie), au bord de la mer). –Horn 1895a: 173; 1926a: 311.–Blackwelder, 1944: 19.–Sumlin, 1979: 115.

Recognition.— The character state combination of large body size 9.0-13.5 mm), elytra completely pale or with almost effaced maculations (Figs. 91a, b), dense appressed white setae covering most of the body, and unidentate labrum distinguishes adults of *C. nivea*.

Description.— *Body length.* Approximately 9.0-13.5 mm M and F.

Body colour. Head and pleuron slightly glossy, coppery and coppery green reflections. Elytra entirely pale or with scattered coppery-green patches. Venter black with coppery or green reflections.

Body setae. Dense white appressed setae on head, frons, clypeus, genae, dorsal side or antennal articles 1,3,4 pronotum (mainly front and lateral portions), pleuron, prosternum, lateral portions of metasternum and metacoxae, legs (sparser on tarsus), and abdominal sterna 1-6 (males), 1-5 (females).

Other external features. Tooth of mentum long. Labrum unidentate with four to 11 (most commonly eight) submarginal setae (Figs. 79a-c). Pronotum broad, hind angles protruding posteriorly, sutures deep (Figs. 85a-c). Coupling sulcus of mesepisternum of female a deep groove. Apex of front trochanters with one sensory seta, middle trochanters glabrous. Elytra with apices slightly recurved, apical spine obsolete; maculations effaced, ground colour completely absent or diffuse; punctation generally small, few large green

or coppery punctures near shoulder and median suture (Figs. 91a, b); microsculpture irregularly isodiametric; apical serrulations small.

Female genitalia. Sternum 8 with shallow V-shaped apical emargination; apices rounded, each with five to seven long thick setae (Figs. 99a, 100a); second gonocoxa with several long and short setae along medial margin (Figs. 99a, 100a); second gonapophyses elongate as in Figures 99a, 100a; syntergum 9 and 10 broadened apically (Figs. 99b, 100b); ventral sclerite lightly sclerotized with posterior lateral projections, median ridge absent (Figs. 99c, 100c); oviduct sclerite wide, with little or no anterior emargination (Figs. 99c, 100c); spermatheca and duct fused to bursa at base, spermatheca and duct *ca* 3.5-4.0 mm (Figs. 99c, 100c).

Male genitalia. Male genitalia have been described by Vidal Sarmiento (1966b: 41).

Geographical Variation and Subspecies.— Most adults in northern localities of Brazil have entirely pale elytra; those in southern localities, in Argentina, have elytra with pigmentation forming a diffuse pattern of elytral maculations. Intermediate populations consist of a majority of adults with varying degrees of pigmentation in the elytra. This characteristic seems to be a reasonable basis for the recognition of two subspecies because a north-south irregular cline is evident. The names *C. nivea nivea* and *C. nivea orbignyi* Guérin-Méneville are retained for northern (Brazil, Uruguay) and southern (Argentina) populations respectively (Fig. 113). The name *C. conspersa*, which was assigned to intermediate forms is not recognized.

Relationships.— *Cicindela nivea* and *C. hirsutifrons* (n. Argentina) are sister species.

Habitat and Period of Activity.— The activity period is from September to June, though most adults examined were collected in October, November, December, January, and February. Populations are probably found close to sea beaches as indicated by the distribution of the species (Fig. 112).

Geographical Distribution, Localities, Examined Specimens.— East coast of South America from Espirito Santo, Brazil south to Patagonia (Fig. 112).

Cicindela nivea nivea Kirby, Brazil. *Espirito Santo*: Gurapari, 13M, 6F, MZSP. *Rio de Janeiro*: Atafona, 1M, 1F, MNRJ; Barra de Marua, Praia de Itapuacu*, 3M, 1F, MZSP; Cidade, 2M, MZSP; Copacabana, 1F, IOC, 2M, 2F, MZSP; Itacuruga*, 1M, IOC; Leblon, 1M, 5F, MNRJ; Niteroi, 3M, 1F, IOC, 1F, MZSP, 2M, 2F, MNRJ; no locality, 12M, 6F, ICCM; Praia do Sai*, 1M, 1F, MNRJ; Recreio dos Bandeirantes*, 1M, 3F, MNRJ; Rio de Janeiro, 1M, 3F, MZSP, 1F, MNRJ; Tijuca, 7M, 4F, MZSP. *Rio Grande do Sul*: Torres, 3M, 1F, MZSP. *Santa Catarina*: Florianopolis, 9M, 3F, MZSP; Itaiaby*, 1F, MZSP; no locality, 1F, IOC, 4M, MZSP. *São Paulo*: Campos do Jordao, 1M, 3F, MZSP; Iguape, 1F, MZSP; Itanhaem, 1M, 5F, MZSP; Peruibe, 1M, 1F, MZSP; Santos, 3M, 6F, IOC, 2F, MZSP, 1M, 1F, MNRJ; São Vincente, 1M, 3F, MZSP.

Uruguay. Atlantida, 1M, MZSP; Montevideo, 2M, 1F, MZSP.

Cicindela nivea orbignyi Guérin-Méneville. Argentina. *Buenos Aires*: Buenos Aires, 1M, 3F, IOC; La Plata 1F, MZSP.

The *melaleuca* group

Adults of this group are characterized by eight to fewer than eight submarginal setae on labrum, and very large foveae on elytra. The group has seven species, two of which are found in Brazil, *C. melaleuca* and *C. patagonica*. The geographical range of the *melaleuca* group is centerd in northern Argentina and extends

northward to southeastern Brazil, western Paraguay and eastern Bolivia, and southward to temperate Patagonia and Chile. The *melaleuca* and *suturalis* groups are a sister pair.

Cicindela (Plectographa) melaleuca Dejean
Figs. 80, 86, 92, 101, 102, 113

Cicindela melaleuca Dejean, 1831: 238 (TYPE LOCALITY, près de Buènos-Ayres, sur les bords de la rivières de La Plata, Argentina). –Horn, 1915: 409; 1926a: 310; 1938: 53.– Barattini, 1929: 1219.– Fernandez, 1936: 107.– Blackwelder, 1944: 18. –Rivalier, 1954: 266.– Vidal Sarmiento, 1966b: 40; 1967: 213.– Sumlin, 1979: 110.

Recognition.— The character state combination of the very dark brown to black body colour, broad pronotum, (Figs. 86a, b), setose vertex, frons, clypeus and genae, and pattern of elytral maculations (Fig. 92) distinguishes specimens of *C. melaleuca* from other Brazilian tiger beetles.

Description.—

Body length. ca 8.5-10.5 mm M, *ca* 9.0-11.0 mm F.

Body colour. Head and pronotum slightly glossy, elytra dull. Dorsum very dark brown or black. Pleuron and sternum black with slight reflections of copper, blue, green, and purple. Abdominal sterna black with slight metallic reflections from lateral margins.

Body setae. Head with vertex, frons, clypeus, and genae setose. Pleuron generally setose, mesepisternum with a few setae near ventral end. Lateral portions of abdominal sterna 1-5 (females' nd 1-6 (males) with appressed setae.

Other external features. Labrum elongate, unidentate, almost tridentate, with six   10 (most commonly eight) submarginal setae (Figs. 80a, b). Pronotum very wide, especially in females, ∪roadened in anterior 0.33 (Figs. 86a, b). Coupling sulcus of mesepisternum of female a straight, long, shallow, broad groove. Apex of front trochanters with one seta. Elytra each with apex recurved to a small spine (Fig. 92). Pattern of elytral maculations with connected humeral lunule and middle band, marginal lunule reduced, apical lunule complete (Fig. 92). Punctation of elytra green, with a row of large foveae, green-blue with bright coppery umbilicate centers, near median suture and a cluster near shoulder (Fig. 92).

Female genitalia. See also Vidal Sarmiento (1967: 209). Sternum 8 with very broad and shallow apical emargination, apices each with five to nine stout setae (Figs. 101a, 102a). Second gonocoxa and second gonapophyses as in Figures 101a, 102a. Syntergum 9 and 10 as in Figures 101b, 102b. Ventral sclerite with two elongate posterior projections (Figs. 101c, 102c). Oviduct sclerite wide (Figs. 101c, 102c). Spermatheca and duct at least 4.5 mm long (broken in dissection).

Male genitalia. Male genitalia have been described by Vidal Sarmiento (1966b: 40).

Geographical Variation.— Body colour, pattern of the elytral maculations and genitalic characteristics vary considerably in Argentina, and distinct geographical populations occur there. *Cicindela melaleuca* is widespread ranging from Patagonia to Rio Grande do Sul. The *C. reedi* Horn form is a conspecific member or close relative that occurs in Patagonia. Horn (1938: 53) is followed by Sumlin (1979: 111) in treating *C. reedi* as a subspecies of *C. melaleuca* though Rivalier (1954: 266) considers it to be a member of *C. drakei* Horn.

Relationships.— *Cicindela melaleuca* and *C. patagonica,* are sister species.

Habitat and Period of Activity.— Adults have been found beside salt marshes in Rio Grande do Sul, at the mouth of the Rio de La Plata, and inland in dry areas (Brullé, 1837: 8), in January and February.

Geographical Distribution, Localities, Examined Specimens.— Coastal southern Brazil, Uruguay, and Argentina (Fig. 113).

Argentina. *Buenos Aires*: Buenos Aires, 1M, 1F, MZSP.
Brazil. *Rio Grande do Sul*: salt marshes, 3F, ICCM.
Uruguay. Montevideo, 3M, 2F, ICCM, 1F, MNRJ.

Cicindela (Plectographa) patagonica Brullé
Figs. 81, 87, 93, 103, 113

Cicindela patagonica patagonica Brullé, 1837: 7 (TYPE, a male in the MNHP general collection bearing the following labels: (green disc)/ "Muséum Paris/Patagonie d'Orbigny/Patagonica/TYPE" (black letters on a red label); TYPE LOCALITY, sur les bords du Rio Negro (Patagonie)). –Horn, 1915: 409; 1926a: 311; 1938: 53.– Barattini, 1929: 1222.– Fernandez, 1936: 108. –Blackwelder, 1944: 19.– Rivalier, 1954: 266.– Vidal Sarmiento, 1966b: 43.– Sumlin, 1979: 114.

Cicindela patagonica cherubim Chevrolat, 1858: 315 (TYPE LOCALITY, des environs de Montevideo).–Horn, 1915: 409; 1926a: 311; 1938: 53.– Barattini, 1929: 1222. –Fernandez, 1936: 108.– Blackwelder, 1944: 19.– Rivalier, 1954: 266.– Vidal Sarmiento, 1966b: 43.– Sumlin, 1979: 114.

Cicindela patagonica bergiana Horn, 1985a: 174 (TYPE LOCALITY, Montevideo); 1915: 409; 1926a: 311; 1938: 53.– Fernandez, 1936: 108. –Blackwelder, 1944: 19.– Rivalier, 1954: 266.– Sumlin, 1979: 114.

Recognition.— The broadly fused pale maculations along lateral margin of the elytron (Figs. 93a, b) combined with a setose clypeus, unidentate labrum bearing seven to nine (eight basic) submarginal setae, large body size (approximately 9.0-10.0 mm), and restricted distribution in southern Rio Grande do Sul distinguish specimens of *C. patagonica* from those of other Brazilian species.

Description.—

Body length. 9.0 mm M, 10.0 mm F.

Body colour. Dorsum ground colour brown. Head, pronotum and elytra with coppery and blue-green reflections.

Body setae. Frons and clypeus setose. Pleuron setose. Proepisternum densely setose; setae on lateral margin of abdominal sternites 1-5.

Other external features. Labrum unidentate with seven to nine (eight basic) submarginal setae (Figs. 81a, b). Pronotum broad with posteriorly protruding hind angles (Figs. 87a, b). Coupling sulcus of mesepisternum of female a deep groove. Apex of front trochanters with a single seta. Elytra somewhat flattened; apices recurved; apical spine small (Figs. 93a, b). Pattern of elytral maculations broad, continuous along lateral margin, but all lunules present and distinct (Figs. 93a, b). Punctation sparse and shallow with row of larger punctures along median suture.

Female genitalia. No females of *C. p. patagonica* or *C. p. bergiana* were available for study thus only genitalia of *C. p. cherubim* were examined. Sternum 8 with V-shaped emargination, apices broadly rounded each with seven or eight long thick setae (Fig. 103a). Second gonocoxa with long setae on apical end (Fig. 103a). Second gonapophyses with medial and lateral portions of equal length (Fig. 103a). Syntergum 9 and 10 as in Figure 103b. Ventral sclerite of bursa broad and lightly sclerotized, median ridge absent (Fig. 103c). Oviduct sclerite with well developed lateral flanges (Fig. 103c). Length of spermatheca and duct approximately 3.5 mm.

Male genitalia. Male genitalia of *C. p. patagonica* and *C. p. cherubim* have been described by Vidal Sarmiento, 1966b.

Geographical Variation and Subspecies.— *Cicindela patagonica bergiana* Horn, a brown form, has been recorded from northern Argentina, Uruguay and Rio Grande do Sul, Brazil by Horn (1915: 409), but no details about the latter record were given. *Cicindela p. cherubim* Chevrolat is a green to blue-green from similar to *C. p. bergiana* in the very broad continuous elytral maculations and occupies Uruguay

and the region of northeastern Argentina near Buenos Aires. The nominate from, *C. p. patagonica,* occurs southward to Patagonia.

Relationships.— *Cicindela patagonica* and *C. melaleuca* are sister species.

Habitat and Period of Activity.— Specimens have been collected in December and February on the seacoast.

Geographical Distribution, Localities , and Examined Specimens.— Coastal from Rio Grande do Sul to Patagonia (Fig. 113). The subspecies *C. p. bergiana* occurs in northern most portions of the range.

Argentina. *Buenos Aires*: Buenos Aires, 3M, IOC. *Santa Cruz*: Santa Cruz, 2M, IOC.

Brazil. *Rio Grande do Sul*: no locality, 1M, BMNH.

Uruguay. Aramincla, 1F, MNRJ; Cuchilla Alta, 1M, MNRJ; Montevideo, 2F, IOC, 3F, MZSP; Rocha, 1F, MNRJ.

The *nigrovittata* group

Adults of this group are characterized by deep rugosity in form of two swirls on head between the eyes. The group has only one species, *C. nigrovittata*, which is found in the Brazilian Highlands. Phylogenetic relationships of the *nigrovittata* group are uncertain.

Cicindela (Plectographa) nigrovittata Horn
Figs. 82, 88, 94, 104, 109, 114

Cicindela nigrovittata Horn, 1896c: 172 (SYNTYPES, two females and one male in the IPZE labelled: "Nonfried Minas Geraes/Type ! Dr. W. Horn (1M 1F), Type ! Coll. W. Horn (1F)/Syntypes" (black letters on red label); TYPE LOCALITY, Minas Geraes); 1915: 405; 1926a: 307; 1938: 52.– Blackwelder, 1944: 19.

Recognition.— The character state combination of the large body size, black body colour, large deep punctures with sharp edges in the anterior 0.5 of the elytra (Fig. 94) and pronotum (Fig. 88), and one or two small pale spots, and velvety patterns on the elytra (Fig. 94) distinguish adults of *C. nigrovittata* from those of other Brazilian species of *Cicindela*. The female genitalia are diagnostic (Figs. 104a-c).

Description.—

Body length. ca 7.5 mm M, *ca* 8.0-9.0 mm F.

Body colour. Dorsum dull, black, matte and velvety patterns on the elytra. Venter slightly glossy, black faint purple reflections from proepisternum and mesepisterna. Legs black, with hint of coppery and green reflections.

Body setae. Fine sparse white pubescence present on: vertex, frons, and genae of head; all margins and beside longitudinal suture of pronotum, pleuron, and lateral portions of abdominal sterna 1-5. Few short fine setae arise from deep punctures on basal end of elytra.

Other external features. Vertex of head deeply rugose. Two wide pits on vertex between hind margins of eyes. Tooth of mentum elongate, well developed. Preapical articles of labial palpi broad. Labrum convex, elongate, tridentate, with four to six submarginal setae (Fig. 82). Pronotum broadened anteriorly, sides not rounded; large, deep punctures on lateral portions (Fig. 88). Coupling sulcus of mesepisternum of female shallow, wide, virtually absent. Apex of front trochanters with one seta. Elytra broadened in apical 0.33; apices slightly recurved to small spine (Fig. 94). Pattern of elytral maculations with one or two small pale

spots, and velvety and matte motif (Fig. 94). Punctures of elytra large, deep, with sharp edges (not raised) in basal 0.33, shallow and indistinct in apical 0.66 (Fig. 94). Microsculpture of elytra basically isodiametric, unclear in matte areas. Apices of elytra almost smooth, microserrulations tiny.

Female genitalia. Sternum 8 with deep moderately wide apical emargination, each apex with five stout setae (Fig. 104a). Second gonocoxa with two or three setae on medial margin (Fig. 104a). Second gonapophyses elongate (Fig. 104a). Syntergum 9 and 10 as in Figure 104b. Bursa copulatrix with pair of lateral extensions (Fig. 104c). Ventral sclerite of bursa with two lateral posterior projections (Fig. 104c). Oviduct sclerite small, shield-shaped (Fig. 104c). Spermatheca and duct at least 2.0 mm long (broken in dissection).

Male genitalia. Median lobe stout, apex short slightly curved ventrally (Figs. 109a, b). Internal sac with flagellum 1.5 loops at base. Tooth dark elongate, narrow, spatulate apex; stylet absent. Small stiffening rib present; shield small. Arciform piece broad; central plate square-shaped at its base; right bar narrow (Figs. 109a-d).

Geographical Variation.— The pale spots on the elytra vary from one to two, and the extent of the velvety pattern on the elytra differs in the few specimens examined. A geographical pattern in these characteristics is not evident.

Relationships.— *Cicindela nigrovittata* is not closely related to any other species of subgenus *Plectographa*.

Habitat and Period of Activity.— Unknown.

Geographical Distribution, Localities, Examined Specimens.— Inland (Fig. 114).

Brazil. *Minas Gerais*: Nonfried*, 1M, 2F (syntypes), IPZE; San Antonio Barranca*, 1F, IPZE.

The *apiata* group

Adults of this group are characterized by stylet tooth long and pointed, and shield reduced or absent from the internal sac of the male. The group has two species, of which one, *C. apiata*, is found in Brazil. The geographical range of the *apiata* group is centered in northern Argentina and extends northward to the Brazilian Highlands. The *apiata* group is relatively primitive and not closely related to other groups in subgenus *Plectographa*.

Cicindela (Plectographa) apiata Dejean
Figs. 83, 89, 95, 105, 106, 110, 111, 114

Cicindela apiata apiata Dejean, 1825: 86 (TYPE LOCALITY, la partie meridionale du Brésil).– Bruch, 1907: 123.– Horn, 1915: 408; 1926a: 310, 1938: 52. –Varas Arangua, 1925: 37.– Barattini, 1929: 1217.– Fernandez, 1936: 107.– Blackwelder, 1944: 16. –Rivalier, 1954: 266.– Vidal Sarmiento, 1966a: 256, 259; 1966b: 39.– Sumlin, 1979: 114.

Cicindela apiata claussenii Putzeys, 1845: 365 (TYPE LOCALITY, la province des Mines au Brésil).– Horn, 1915: 408; 1923: 111; 1926a: 310; 1938: 52. –Blackwelder, 1944: 16.– Rivalier, 1954: 266.– Vidal Sarmiento, 1966b: 39.

Recognition.— Adults of *C. apiata* are set apart from those of other Brazilian species by a combination of the broad elytral maculations lacking a marginal band (Figs. 95a-d), narrow unidentate labrum with seven to 13 submarginal setae (Figs. 83a-d), and structure of female genitalia (Figs. 105, 106). The male genitalia are also specific (Figs. 110, 111, and Vidal Sarmiento, 1966b: 33, 39).

Synonyms.— Names were based upon comparison of specimens on loan with original descriptions.

Description.—

Body length. 7.0-9.5 mm M, 7.5-9.5 mm F.

Body colour. Dorsum dull, dark brown. Head and pronotum greenish in some specimens. Pleuron and lateral edges of abdomen mainly coppery. Venter black with blue-green reflections.

Body setae. Pleuron moderately setose. Mesepisternum sparsely setose near coxa. Lateral portions of abdominal sterna 1-6 (males) and 1-6 or 1-5 (females) setose.

Other external features. Labrum unidentate, tooth prominent or obscurely tridentate, seven to 13 submarginal setae (Figs. 83a-d). Pronotum stout broader in anterior 0.5, sides slightly to strongly ampliate (Figs. 89a-d). Coupling sulcus of mesepisternum of female a broad groove. Apex of front trochanters with one seta. Profemora and mesofemora with very long fine setae. Apices of elytra not recurved, obliquely truncated to tapered, apical spine small. Elytra with maculations broad, with or without ragged edges and appearing as spots or not. Humeral lunule complete, oblique joined or not to complete middle band, apical lunule complete and separate, marginal band absent (Figs. 95a-d). A few setae present or not on shoulder of elytra. Punctation green, sparse with larger umbilicate punctures near shoulder and along median suture. Microsculpture isodiametric bead-like.

Female genitalia. Sternum 8 with moderately deep V-shaped posterior emargination, apices each with three to five stout setae (Figs. 105a, 106a). Second gonocoxa with a few setae on medial margin (Figs. 105, 106a). Second gonapophyses as in Figures 105a, 106a. Syntergum 9 and 10 elongate, broadened apically (Figs. 105b, 106b). Ventral sclerite of bursa copulatrix with two posterior lateral extensions (Figs. 105c, 106c). Lateral flanges of oviduct sclerite well developed (Figs. 105c, 106c). Spermatheca and duct *ca* 2.5 mm long.

Male genitalia. Apex of median lobe with small projection (Figs. 110a, b, 111a, b). Internal sac with flagellum 1.5 loops at base. Stylet and tooth both very long and pointed. Right bar and small stiffening rib present; arciform piece moderately wide (Figs. 111c, d and Vidal Sarmiento, 1966b: 33, 39).

Geographical Variation and Subspecies.— Adults of *C. apiata* are varied in body size, in presence or absence of setae on the clypeus, in number of submarginal setae on the labrum, in shape of pronotum, in the pattern of elytral maculations, in presence or absence of setae on the base of elytra; and in presence or absence of setae on sternum 6 of females. Although the specimens used in this study were too few for statistical analysis, the sparse data assembled indicate geographical patterns in the variation of these characteristics.

The body length of *C. apiata* varies from 7.0-7.5 (male) and 7.5-8.0 mm (female) in Rio de Janiero to 9.0-9.5 mm (male) and 9.5 mm (female) in Rio Grande do Sul. In Brazil an uneven southward increase in adult body length is evident with an abrupt change in Rio Grande do Sul. An east-west pattern of variation in body length is not apparent. Adults of both sexes from Argentina are the largest being *ca* 9.0-10.0 mm long.

Variation in the other observed characteristics roughly complements that of body length. Most large specimens have a pronotum with ampliate sides, glabrous clypeus, bear fewer submarginal setae on the labrum (7-8 for males, 8 for females in Rio Grande do Sul; 10 for males, 9 for females in Rio de Janiero), lack setae on the base of elytra, and they have expanded elytral maculations with ragged and spotted edges particularly in the humeral lunule and marginal band which are connected or almost connected. Females lack setae on the lateral margins of abdominal sternum 6.

In contrast, most small specimens have a less stout pronotum with only slightly ampliate sides, bear setae on the clypeus, (usually 2, crossed), have a greater number

of submarginal setae on the labrum (eight or nine for males, 11-12 for females in Rio de Janiero; 11 for males, 13 for females in São Paulo), bear setae on the base of the elytra, and have narrower elytral maculations with even edges and generally unspotted with unconnected humeral lunule and middle band. Females have a few setae on the lateral margins of abdominal sternum 6.

Because there is a considerable amount of concordant variation among these characteristics two subspecies are recognized, *C. apiata apiata* and *C. apiata claussenii*. The former comprises relatively large adults, most of which have a glabrous clypeus, labrum with seven to 10 (males) and eight or nine (females) submarginal setae (Figs. 83a,b), broad pronotum with ampliate sides (Figs. 89a,b), expanded, merged, ragged and spotted elytral maculations (Figs. 95a, b), and glabrous base of elytra and lateral margin of abdominal sternum 6; the female genitalia are as in Figures 105a-c. Adults of the latter subspecies are smaller, most of which have one or two setae on the clypeus, labrum with eight to 11 (males) and 11-13 (females) submarginal setae (Figs. 83c, d), pronotum with sides not noticeably ampliate (Figs. 89c, d), and elytral maculations relatively narrow, with an even outline, isolated maculations, and few spots (Figs. 95c, d), and a few setae on the base of elytra and lateral margin of abdominal sternum 6. Female genitalia are as in Figures 106a-c.

The subspecies *C. a. apiata* ranges from the northern half of Argenti   and Uruguay north to Rio Grande do Sul, Matto Grosso, São Paulo, Minas Gera   and Rio de Janiero, while *C. a. claussenii* occurs in Matto Grosso, São Paulo, Minas Gerais, and Rio de Janiero (Fig. 114). Adults with characteristics of both subspecies are present in Rio de Janiero.

Relationships.— *Cicindela apiata* and *C. eugeni* Castelnau (n. Argentina) are sister species.

Habitat and Period of Activity.— Adults have been collected from October to May, beside water, at various elevations from sea level to 1700 m. Adults of *C. a. apiata* have been found near salt marshes.

Geographical Distribution, Localities, Examined Specimens.— Coastal and inland, from the northern half of Argentina north to Rio Grande do Sul, São Paulo, Matto Grosso, Minas Gerais, and Rio de Janiero (Fig. 114).

Cicindela apiata apiata Dejean. Brazil. *Matto Grosso*: Salobra, 1M, MZSP; Três Lagoas, 5M, MZSP; Vacaria, 1M, 1F, MZSP. *Minas Gerais*: Mar de Espanha*, 2F, IOC, 1M, 1F, MZSP; Passa Quatro, 1M, 2F, IOC. *Rio de Janeiro*: Campo Bello*, 1F, MZSP; Itatiaia (700-1110m), 2M, 7F, IOC; Rio de Janeiro, 1M, 1F, MZSP. *Rio Grande do Sul*: salt marshes, 4M, 1F, ICCM. *São Paulo*: Campos do Jordao, 1M, 3F, MZSP; Cantareira*, 1M, MZSP; Garca, 6M, 1F, MZSP; Onda Verde*, 2F, MZSP; Pindamonhangaba, 1M, 1F, MZSP.

Cicindela apiata claussenii Putzeys. Brazil. *Matto Grosso*: Vacaria, 4M, 4F, MZSP. *Minas Gerais*: Caraga*, 1M, IOC; Pocos de Caldas, 12 !, RRMC: Virginia (1500 m), 1M, MNRJ. *Rio de Janeiro*: Grajau, 1M, 1F, IOC; Itatiaia, 1M, 1F, MNRJ; Petropolis, 1M, MNRJ; no locality, 3M, 2F, ICCM. *São Paulo*: Alto da Serra (mountains between São Paulo and Santos), 5M, 6F, MZSP; Serra do Bocaina*, 7M, 4F, MNRJ.
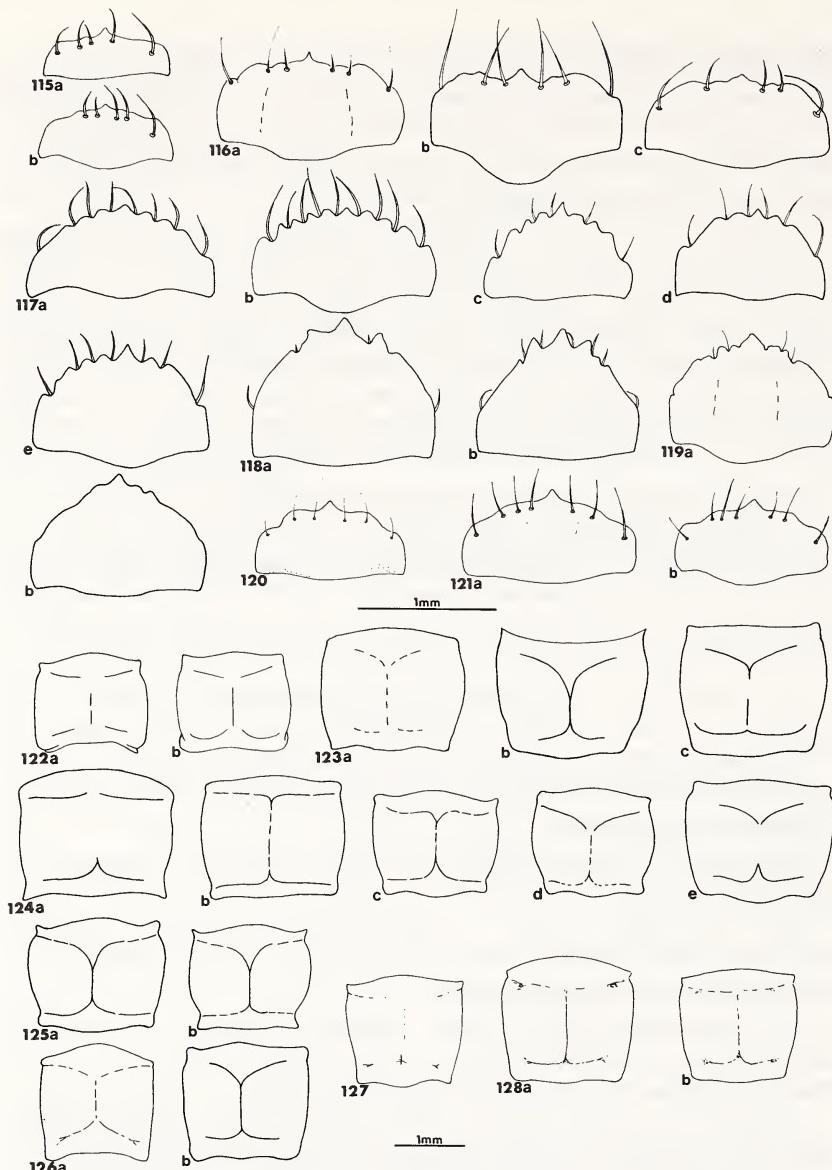
Figs. 115–121. Labrum, dorsal aspect: 115, *Cicindela kollari* Gistl, Santa Teresina, M. Grosso: (a) female; (b) male; 116, *C. confluentesignata* Horn: (a) female, Minas Gerais; (b) female, (c) male, Rivera, Uruguay; 117, *C. morio* Klug: (a) female, (b) male, Jatai, Go.; (c) female, (d) male, Dianopolis, Go.; (e) female, Pará; 118, *C. marquardti* Horn, Três Lagoas, M. Grosso: (a) female; (b) male; 119, *C. piligera* Horn: (a) male, Minas Gerais; (b) female, Ecuador; 120, *C. obsoletesignata* Horn, male, Santa Catarina; 121, *C. friedenreichi* Dokhtouroff, Rio Grande do Sul: (a) female; (b) male. Figs. 122–128. Pronotum, dorsal aspect. 122, *Cicindela kollari* Gistl, Santa Teresina, M. Grosso: (a) female; (b) male; 123, *C. confluentesignata* Horn: (a) female, Minas Gerais; (b) female, (c) male, Rivera, Uruguay; 124, *C. morio* Klug: (a) female, (b) male, Jatai, Go.; (c) female, (d) male, Dianopolis, Go.; (e) female, Pará; 125, *C. marquardti* Horn, Três Lagoas, M. Grosso: (a) female; (b) male; 126, *C. piligera* Horn: (a) male, Minas Gerais; (b) female, Ecuador; 127, *C. obsoletesignata* Horn, male, Santa Catarina; 128, *C. friedenreichi* Dokhtouroff, Rio Grande do Sul: (a) female; (b) male.
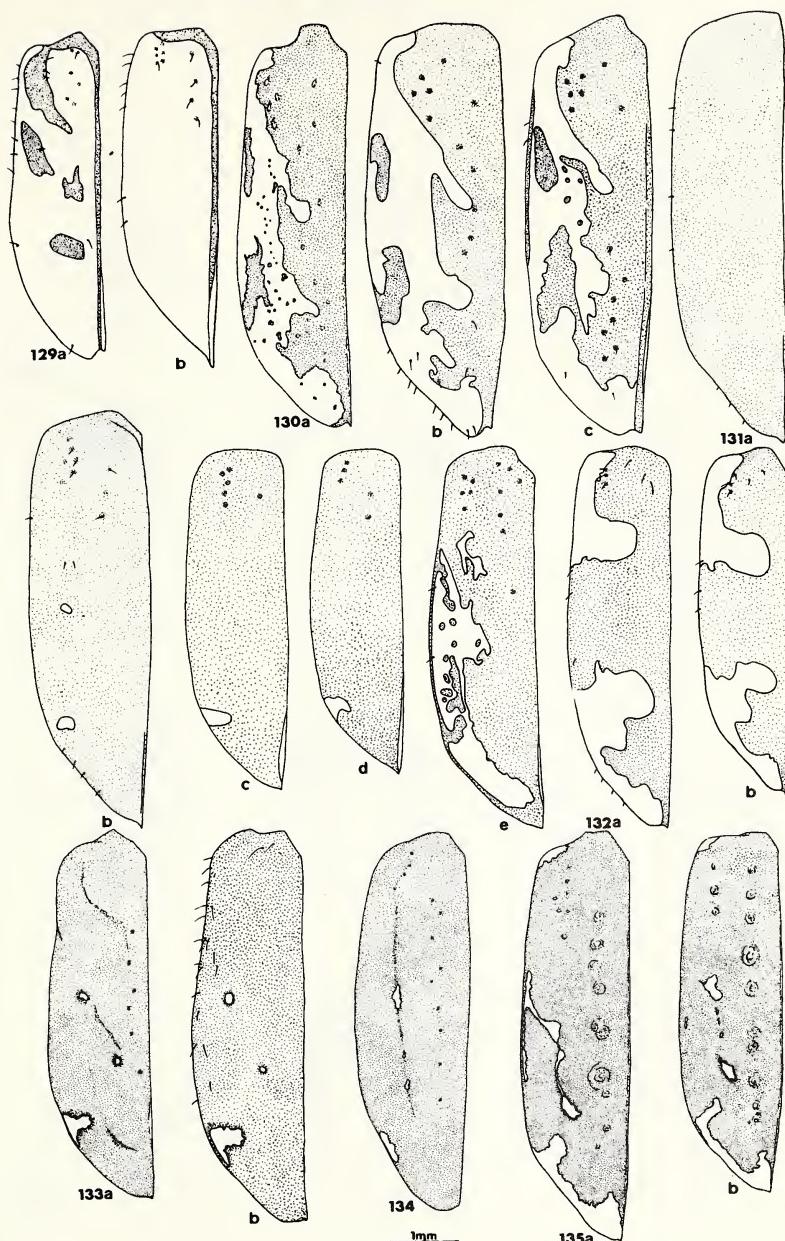
Figs. 129–135. Elytron, dorsal aspect. 129, *Cicindela kollari* Gistl, Santa Teresina, M. Grosso: (a) female; (b) male; 130, *C. confluentesignata* Horn: (a) female, Minas Gerais; (b) female, (c) male, Rivera, Uruguay; 131, *C. morio* Klug: (a) female, (b) male, Jatai, Go.; (c) female, (d) male, Dianopolis, Go.; (e) female, Pará; 132, *C. marquardti* Horn, Três Lagoas, M. Grosso: (a) female; (b) male; 133, *C. piligera* Horn: (a) male, Minas Gerais; (b) female, Ecuador; 134, *C. obsoletesignata* Horn, male, Santa Catarina; 135, *C. friedenreichi* Dokhtouroff, Rio Grande do Sul: (a) female; (b) male.
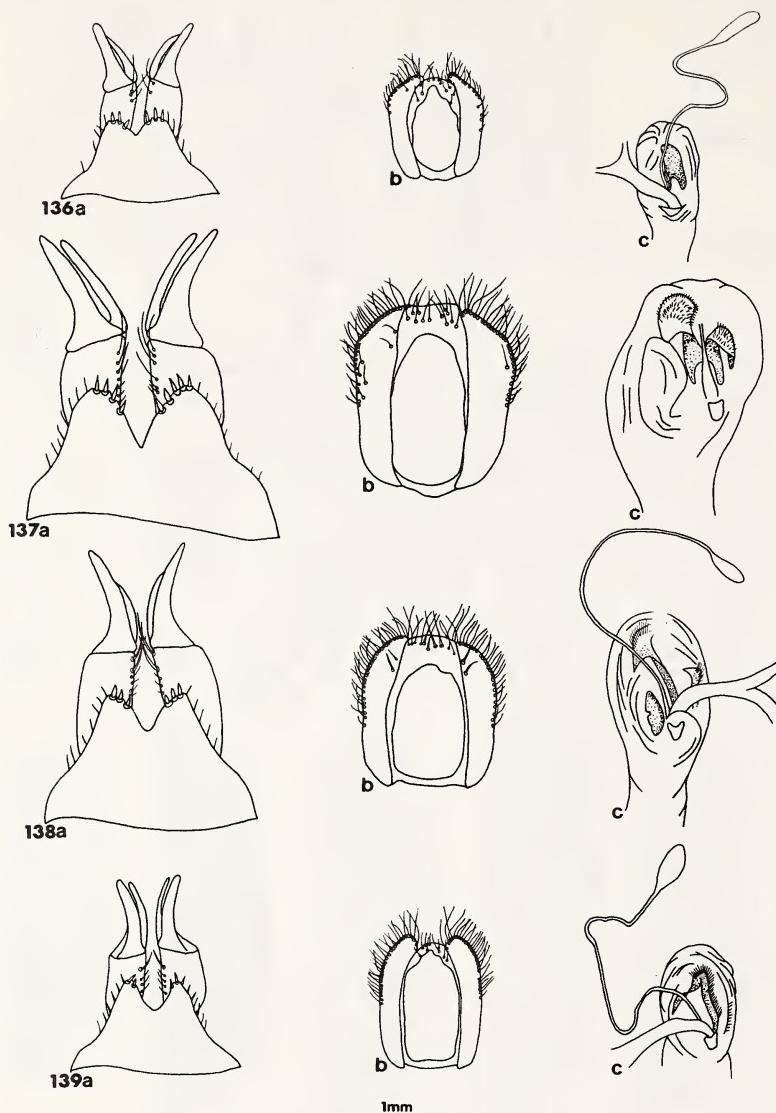
Figs. 136–139. Female genitalia: (a) sternum 8, second gonocoxa, second gonapophyses, ventral aspect; (b) syntergum, 9 & 10, dorsal aspect; (c) bursa copulatrix, oviduct sclerite, oviduct, spermatheca and duct, ventral sclerite, ventral aspect. 136, *Cicindela kollari* Gistl, Santa Teresina, M. Grosso; 137, *C. confluentesignata* Horn: Rivera, Uruguay; *C. morio* Klug: 138, Jatai, Go.; 139, Dianopolis, Go.;
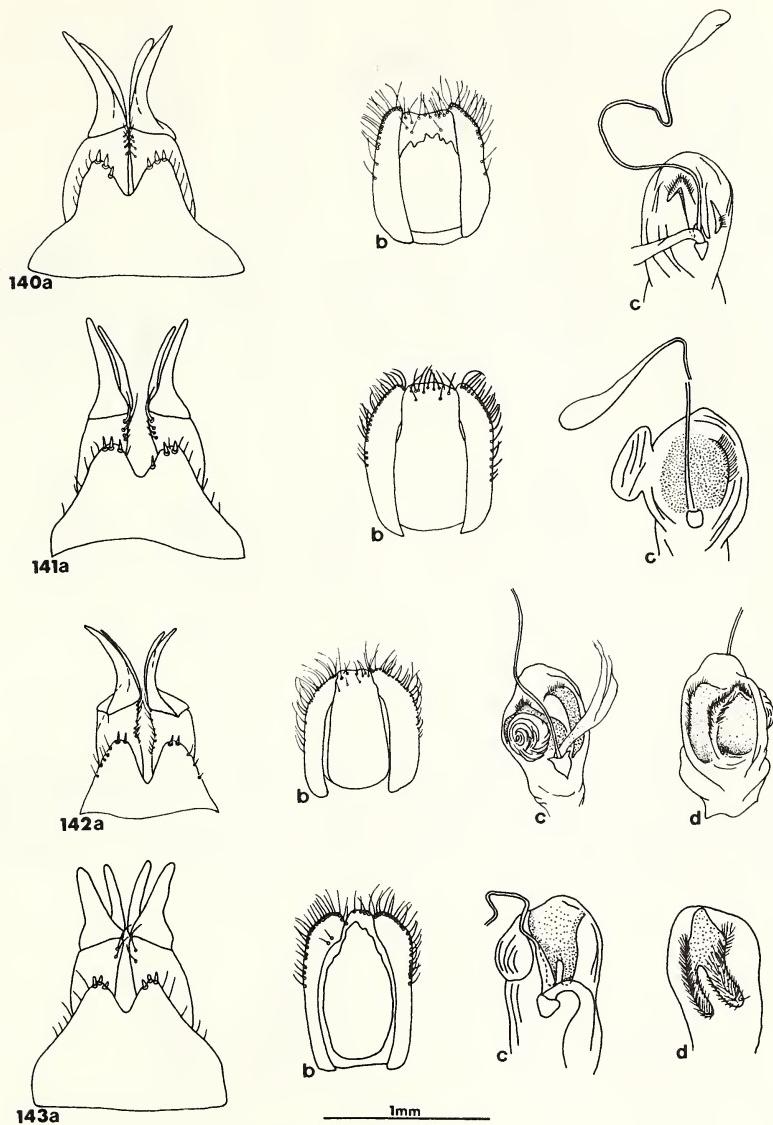
Figs. 140–143. Female genitalia: (a) sternum 8, second gonocoxa, second gonapophyses, ventral aspect; (b) syntergum, 9 & 10, dorsal aspect; (c) bursa copulatrix, oviduct sclerite, oviduct, spermatheca and duct, ventral sclerite, ventral aspect; (d) dorsal aspect. *Cicindela morio* Klug: 140, Pará; *C. marquardti* Horn: 141, Três Lagoas, M. Grosso; 142, Matto Grosso or São Paulo (syntype); *C. piligera* Horn: 143, Ecuador.
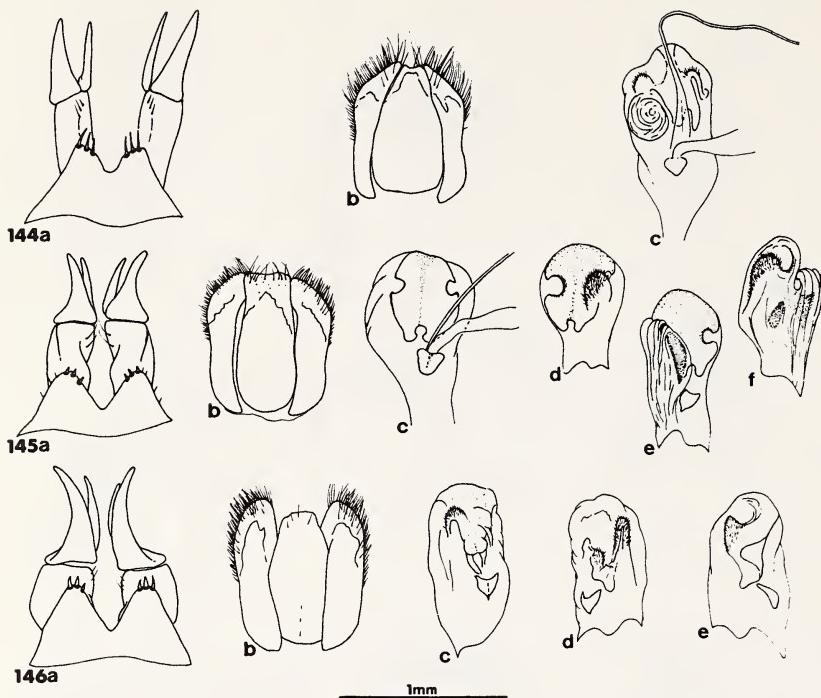
Figs. 144–146. Female genitalia: (a) sternum 8, second gonocoxa, second gonapophyses, ventral aspect; (b) syntergum, 9 & 10, dorsal aspect; (c) bursa copulatrix, oviduct sclerite, oviduct, spermatheca and duct, ventral sclerite, ventral aspect; (d) dorsal aspect; (e) left lateral aspect; (f) right lateral aspect. 144, *Cicindela piligera* Horn, Minas Gerais; 145, *C. obsoletesignata* Horn, Santa Catarina; 146, *C. friedenreichi* Dokhtouroff, Rio Grande do Sul.
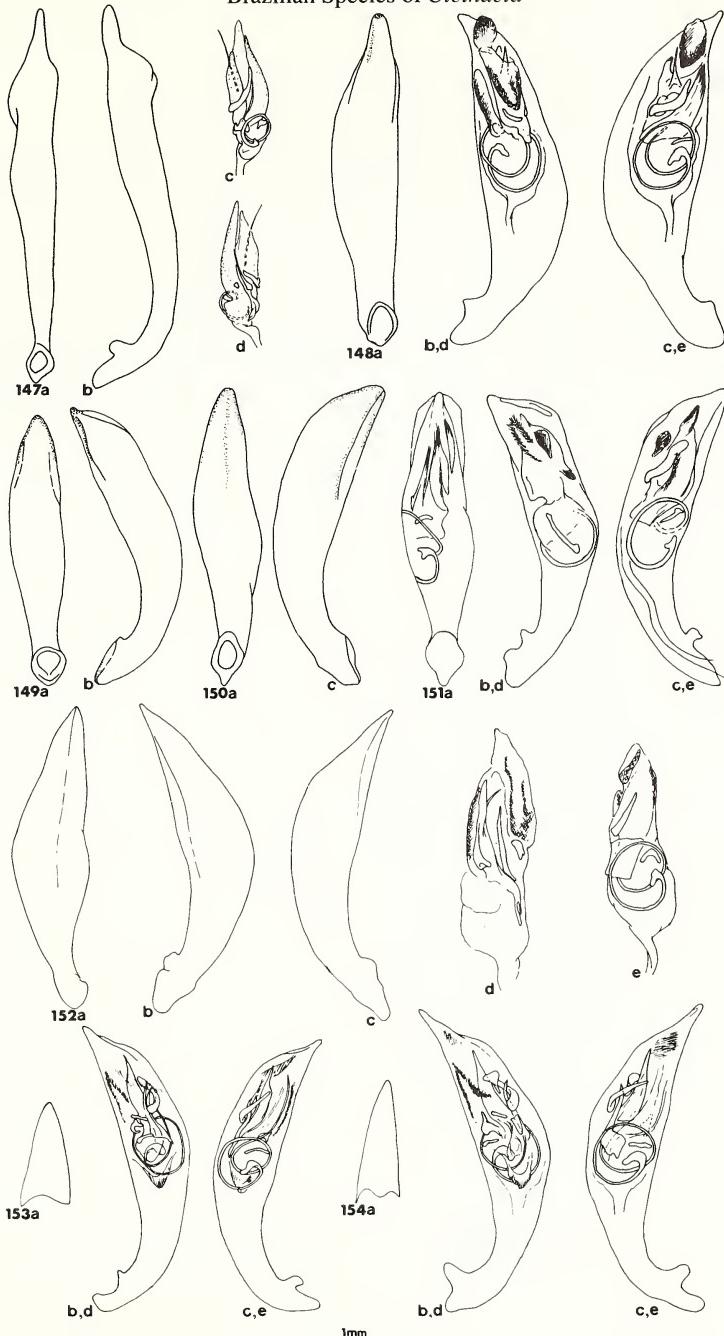
Figs. 147–154. Male genitalia: (a) dorsal aspect (apex only in some specimens), (b) right lateral aspect, (c) left lateral aspect; internal sac, arciform piece, central plate, flagellum, right bar, small stiffening rib, stylet, tooth, (d) right lateral aspect, (e) left lateral aspect. 147, *Cicindela kollari* Gistl, Santa Teresina, M. Grosso; *C. morio* Klug: 148, Jatai, Go.; 149, Dianopolis; *C. marquardti* Horn: 150, Três Lagoas, M. Grosso; 151, Matto Grosso or São Paulo (syntype); 152, *C. piligera* Horn, Minas Gerais; 153, *C. obsoletesignata* Horn, Santa Catarina; 154, *C. friedenreichi* Dokhtouroff, Rio Grande do Sul.

Fig. 155. Map showing the geographical distribution of the species *Cicindela kollari* Gistl (■), and *C. confluentesignata* Horn (●). Open squares and circle repre⁻   state records of *C. kollari* Gistl and *C. confluentesignata* Horn respectively.

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Fig. 156. Map showing the geographical distribution of the species *Cicindela morio* Klug (●), and *C. marquardti* Horn (■). Open circle represents a state record for *C. morio* Klug.

Fig. 157. Map showing the geographical distribution of the species of *Cicindela friedenreichi* Dokhtouroff (▲). Open circles and squares represent state or country records for *C. piligera* Horn and *C. obsoletesignata* Horn respectively.

Subgenus *Cylindera* Westwood

Genus *Cylindera* Westwood, 1831: 300 (TYPE SPECIES, *Cicindela germanica* Linnaeus, by original designation).–Horn, 1915: 236, 245 and 291. –Rivalier, 1954: 264.– Reichardt, 1977: 374.

Genus *Cicindosa* Motschulsky, 1864: 173 (TYPE SPECIES, *Cicindosa obliquealba* Motschulsky, by original designation). –Horn, 1915: 236, 405.– Reichardt, 1977: 374. NEW SYNONYMY.

Recognition.— Adults of this subgenus are distinguished by the five characters given in couplet 5 of the key. In addition the labrum has 5-13 submarginal or marginal setae; elytral maculations are broad in specimens of most species, extensive in specimens of a few species, and absent in others; apex of the median lobe of the male is not hooked; females of most species have a bursa copulatrix with a well developed ventral sac, and ventral sclerite with two anterior lobes and posterior projections covered with setae; the spermatheca and duct together are approximately 1.7-3.0 mm long.

Species Groups.— This subgenus has two South American species groups, *morio* group and *friedenreichi* group, which together have nine species. Both groups are found in Brazil.

Geographical Distribution.— The geographical range of this subgenus extends from northern Argentina northward to the Amazon River.

Phylogenetic Relationships.— *Cylindera* and *Plectographa* are sister subgenera.

The *morio* group

Adults of this group are characterized by a broad pronotum and membranous tooth in the internal sac of the male. The group has six species, four of which are found in Brazil, *C. kollari, C. confluentesignata, C. morio,* and *C. marquardti.* The geographical range of the *morio* group extends from eastern Brazil to eastern Peru and Ecuador, and southern parts of the Amazon basin. The *morio* group and *friedenreichi* group are a sister pair.

Cicindela (Cylindera) kollari Gistl
Figs. 115, 122, 129, 136, 147, 155

Cicindela hirticollis Dejean, 1831: 256 (not Say) (TYPE LOCALITY, au Brésil).– Gistl, 1837: 64.– Horn, 1915: 404; 1926a: 306.– Blackwelder, 1944: 18.

Cicindela kollari Gistl, 1837: 64 (TYPE LOCALITY, circa Pará in Brasilia).– Horn, 1915: 404; 1926a: 306; 1938: 52. –Blackwelder, 1944: 18.– Rivalier, 1954: 265.

Cicindela scutellaris Gistl, 1837: 87 (not Say) (TYPE LOCALITY, in Brasilia).– Horn, 1915: 404, 1926a: 306.– Blackwelder, 1944: 18.

Cicindela dimidiaticornis Lucas, 1857: 30 (TYPE LOCALITY, le Brésil intérieur).– Horn, 1915: 404; 1926a: 306. –Blackwelder, 1944: 18.

Recognition.— The character state combination of the dark head and pronotum contrasting with the paler elytra, antenna with pale articles 5-11, unidentate short labrum with 5 or 6 submarginal setae (Figs. 115a, b), single seta on the front and middle trochanters, widely expanded elytral maculations (Figs. 129a, b), and large

and deep brown punctures of the elytra distinguishes adults of *C. kollari* from those of other Brazilian species of *Cicindela*.

Adults of *C. kollari* are similar to those of its Peruvian sister species of *C. malaris* Horn which is found in the area of the upper Amazon River system from Pampa del Sacramento to Pebas. Adults of *C. malaris* have a distinct pattern of elytral maculations with large patches of dark colour. Males have appressed white setae on the margins of sterna 1-6. Adults of *C. kollari* have almost or completely immaculate elytra, and males have margins of abdominal sterna 1-5 setose.

Synonyms and Types.— The name *C. dimidiaticornis* was assigned to male of *C. kollari* (see Geographical Variation and Sexual Dimorphism section).

Description.—

Body length. ca 6.8-7.0 mm M, *ca* 6.5 mm F.

Body colour. Head green, coppery and purple (especially females). Pronotum coppery and green. Elytra, mainly ivory, with brown punctation, dark brown patches with hint of blue-green reflections in females. Venter dark brown coppery and green reflections.

Body setae. Males more densely setose than females. Head glabrous. Pronotum margins densely setose disc sparsely setose. Pleuron densely setose, mesepisternum with a few setae near mesocoxa. Lateral portions of abdominal sterna 1-5 in males, 1-6 in females, metasternum and metacoxa with dense appressed setae.

Other external features. Antennal articles 5-11 pale. Labrum narrow (not elongate), unidentate, five or six submarginal setae (Figs. 115a, b). Pronotum square, hind angles of females protruded (Figs. 122a, b). Coupling sulcus of mesepisternum of female an elongate straight groove. Legs, especially the femur, more densely setose in males. Apices of front and middle trochanters each with one seta. Apex of elytra recurved to small spine in females, not recurved elongated to long spine in males (Figs. 129a, b). Dark portions of colour pattern almost effaced or effaced in males (Fig. 129b), patches of dark ground colour indicate oblique humeral lunule and middle band in females (Fig. 129a). Punctures of elytra large, deep, and brown, a few large punctures near shoulder and median suture in basal 0.33. Microsculpture of elytra almost effaced.

Female genitalia. Sternum 8 with shallow, broad, V-shaped apical emargination, apices broadly rounded each with three stout setae (Fig. 136a). Second gonocoxa with several setae on median margin (Figs. 136a). Second gonapophyses as in Figure 136a. Syntergum 9 and 10 as in Figure 136b. Ventral sclerite lightly sclerotized with lateral lobes extending posteriorly (Fig. 136c). Oviduct sclerite short and wide (Fig. 136c). Spermatheca and duct *ca* 1.7 mm long.

Male genitalia. Median lobe tapered apically (Figs. 147a, b). Internal sac with flagellum 1.5 loops at base. Tooth mainly dark elongate membranous field with small sclerite at base. Right bar, stylet and small stiffening rib well developed; shield membranous. Arciform piece moderately wide; central plate lightly sclerotized (Figs. 147c, d).

Geographical Distribution and Sexual Dimorphism.— Insufficient material was available to determine patterns of geographical variation, however, within populations sexual dimorphism occurs. Males have dense body pubescence, non-protruding hind angles of pronotum, almost effaced or completely effaced colour pattern of elytra, and elongate, not recurved, apices of elytra. Females have moderately pubescent bodies, protruding hind angles of pronotum, elytra with extensive patches of dark ground colour and recurved apices.

Relationships.— *Cicindela kollari* and *C. malaris* Horn (Peru) are tentative sister species.

Habitat and Period of Activity.— Adults have been collected in August on the Matto Grosso side of Rio Araguaia, Santa Isabel. Habitat unknown.

Geographical Distribution, Localities, Examined Specimens.— Gentral Brazil (Fig. 155).

Brazil. *Goiás*: no locality, 3!, MNHP. *Matto Grosso*: Santa Isabel, 1M, CASC; Santa Teresina, 1M, 2F, CASC. *Pará*: no locality, 1M, ICCM.

Cicindela (Cylindera) confluentesignata Horn
Figs. 116, 123, 130, 137, 155

Cicindela confluens Horn, 1893: 197 (not Bremi, Fowler, Kraatz); 1894: Pl. 3, Fig. 6.– Blackwelder, 1944: 17.

Cicindela confluentesignata Horn, 1915: 407 (replacement name) (HOLOTYPE, a female in the IPZE collection bearing the following labels: "Minas Geraes, Staudinger/Type ! Dr. W. Horn/Holotypus (black letters on red label)/"*Cicindela confluens* Horn""; TYPE LOCALITY, Minas Geraes); 1926a: 309; 1938: 52.– Fernandez, 1936: 106.– Blackwelder, 1944: 17.– Rivalier, 1954: 265. –Vidal Sarmiento, 1966a: 259; 1966b: 33, 38.– Mandl, 1973: 296 (*Brasiliella*).– Sumlin, 1979: 105.

Recognition.— The character state combination of pattern of elytral maculations (Figs. 130a-c) and the shape of the labrum with its nearly marginal five or six setae (Figs. 116a-c) distinguishes adults of *C. confluentesignata* from other Brazilian species of *Cicindela*.

Synonyms and Types.— Horn (1915: 407) designated the name *C. confluentesignata* for the name *C. confluens* Horn preoccupied by *C. confluens* Kraatz.

Description.—

Body length. 8.5 mm M, 8.5-9.0 mm F.

Body colour. Dorsum slightly glossy; head and pronotum black or dark brown with coppery green reflections; elytra coppery brown with coppery and green reflections and with a few large green punctures. Venter and pleuron glossy, black with blue-green and coppery reflections.

Body setae. Genae with a few setae. Proepisternum moderately setose; mesepisternum with a few setae near ventral end; metepisternum setose. Abdominal sterna 1-6 setose laterally.

Other external features. Antenna with articles 5-11 pale. Labrum convex, basically unidentate but can be up to seven dentate, with five or six marginal setae (Figs. 116a-c). Pronotum stout widest in front 0.5 (Figs. 123a-c). Coupling sulcus of mesepisternum of female a long and narrow groove. Apex of front trochanters each with one seta. Elytra with apices recurved to a short spine; maculations broad and more or less continuous; large and small punctures with green reflections (Figs. 130a-c).

Female genitalia. Sternum 8 with sharp V-shaped emargination in apical end; apices with four or five stout setae of moderate length (Fig. 137a). Second gonocoxa with setae along median margin (Fig. 137a); second gonapophyses narrow and elongate (Fig. 137a); syntergum 9 and 10 as in Figure 137b; ventral sclerite lightly sclerotized with two lateral extensions directed posteriorly, and two anterior flaps covered with brown setae (Fig. 137c); oviduct sclerite small, rectangular (Fig. 137c); spermathecal duct broken, length unknown.

Male genitalia. The male genitalia have been described by Vidal Sarmiento (1966b: 33, 38).

Geographical Variation.— There is local and geographical variation in the pattern of elytral maculations (Figs. 130a-c) and in the shape of the labrum (Figs. 116a-c). Distinct geographical patterns are unclear.

Relationships.— *Cicindela confluentesignata* and *C. granulipennis* Bates (Ecuador) are tentative sister species.

Habitat and Period of Activity.— Adults have been collected in November and January. Habitat unknown. This species may be riparian.

Geographical Distribution, Localities, Examined Specimens.— The species *C. confluentesignata* ranges from Minas Gerais south to Uruguay, northern Argentina and Paraguay (Fig. 155).

Brazil. *Minas Gerais*: no locality, 1F (holotype), IPZE. *Rio Grande do Sul*: Pelotas, 1F, MNRJ.
Uruguay. Durazno, 1M, MNRJ; Rivera, 1M, 3F, MNRJ; Tacuarembo, 1M, MNRJ.

Cicindela (Cylindera) morio Klug
Figs. 117, 124, 131, 138, 139, 140, 148, 149, 156

Cicindela denticulata Klug, 1834: 15 (TYPE LOCALITY, aus Brasilien).– Horn, 1892b: 213; 1915: 405; 1923: 112; 1926a: 307; 1938: 52. –Blackwelder, 1944: 18.– Rivalier, 1954: 265.

Cicindela morio Klug, 1834: 16 (TYPE LOCALITY, aus Brasilien).– Horn, 1892b: 213; 1915: 405; 1926a: 307; 1938: 52. –Blackwelder, 1944: 18.– Rivalier, 1954: 265.– Vidal Sarmiento, 1966a: 259; 1966b: 27.– Sumlin 1979: 108.

Cicindela ocskayi Gistl, 1837: 22 (TYPE LOCALITY, in Brasilia).– Horn, 1915: 405; 1926a: 307.– Blackwelder, 1944: 18.

Cicindela acompsa Chaudoir, 1852: 27 (TYPE LOCALITY, les bords du fleuve des Amazones); 1854: 122. –Horn, 1915: 405; 1926a: 307; 1938: 52.– Blackwelder, 1944: 18.

Cicindela egena Chaudoir, 1854: 123 (TYPE LOCALITY, les contrées riveraines du fleuve des Amazones). –Horn, 1915: 405; 1926a: 307.– Blackwelder, 1944: 18.

Cicindosa obliquealba Motschulsky, 1864: 173 (TYPE LOCALITY, Des rives du fl. des Amazones).– Horn, 1915: 405; 1926a: 307.– Blackwelder, 1944: 18.

Cicindosa inaequalis Motschulsky, 1864: 174 (TYPE LOCALITY, De l'Amérique equatoriale).– Horn, 1915: 405; 1926a: 307.– Blackwelder, 1944: 18.

Recognition.— The character state combination of the elongate, convex, and 7-12 dentate labrum (Figs. 117a-e), black body, pattern of elytral maculations (Figs. 131a-e), and structure of male and female genitalia distinguishes adults of *C. morio* from those of other Brazilian species.

Synonyms and Types.— We have not seen the type of *C. morio*. The name is based upon comparison of the original description with specimens on loan.

Description.—

Body length. 6.5-10.0 mm M and F.

Body colour. Dorsum dull, black, metallic reflections faint, matte patterns on elytra. Pleuron and venter semi-glossy to glossy, black, metallic reflections more obvious.

Body setae. Pleuron setose (appressed mainly). Lateral portions of abdominal sterna one to six in males and one to five in females with sparse to moderately dense appressed setae.

Other external features. Antennal articles 5-6 paler than 1-4 and 7-11. Labrum elongate, convex seven to 12-dentate (basically nine); deep marginal notches each with one marginal seta (eight to 10 setae total) (Figs. 117a-e). Pronotum widest in anterior 0.5, sutures shallow (Figs. 124a-e). Coupling sulcus of mesepisternum of female a broad groove. Apex of front and middle trochanters with a single sensory seta. Elytra with small apical spine. Pattern of elytral maculation varies from completely immaculate to extensive, but with pale maculations lacking on the front part of the shoulder (Figs. 131a-e). Punctures of elytra shallow, green.

Female genitalia. Sternum 8 with deep V-shaped apical emargination, each apex with two or three thick setae. Median margin of second gonocoxa with row of setae (Figs. 138a, 139a, 140a). Syntergum 9 and 10 as in Figures 138b, 139b, 140b. Ventral sclerite in one piece, or two parts, a central one with recurved apex (anvil-shaped in lateral aspect), and left lateral flattened piece; setose (Figs. 138c, 139c, 140c). Oviduct sclerite shield-shaped (Figs. 138c, 139c, 140c). Bursa with small ventral sac on right side (Figs. 138c, 139c, 140c). Spermatheca and duct *ca* 1.75 mm long.

Male genitalia. Median lobe stout with short tapered apex (Figs. 148a-c, 149). Internal sac with flagellum 1.5 loops at base (Figs. 148d, e). Tooth elongate field. Arciform piece large. Stylet large (Figs.

148d, e). Right bar and small stiffening rib well developed 9Figs. 148d, e). Two or three apical brush-like patches (Figs. 148d, e).

Geographical Variation.— A considerable amount of variation occurs in body size, dentition and number of submarginal setae of the labrum, and pattern of the elytral maculations, but geographical patterns are unclear. Variation in these characteristics was considerable in the Santarem population sample. Adults of the *C. acompsa* form which have extensive pale maculations on the elytra are not given subspecific status as they are found with conspecific adults which have various elytral patterns.

Relationships.— *Cicindela morio* and *C. marquardti* are sister species.

Habitat and Period of Activity.— Adults are active beside fresh water from October to January. One specimen was collected in June.

Geographical Distribution, Localities, Examined Specimens.— Inland, from Amazon River south to Matto Grosso, Brazil (Fig. 156).

Brazil. *Amazonas.* Manaus, 1M, INPA, 1M, 1F, IOC; Manaus (1 km w. Taruma Falls), 1F, ICCM; Manaus (Bisego L.), 1M, MZSP; no locality, 3M, 1F, INPA. *Goiás*: Chapada, 5M, 5F, ICCM; Dianopolis, 8M, 10F, MZSP; Jatai, 1M, 1F, BMNH, 2M, 2F, MZSP. *Matto Grosso*: Barra do Tapirapes, 1F, CASC, 1M, MZSP; Corumba, 1M, MZSP; Utiariti, 1M, MZSP. *Pará*: Belem, 1M, CASC; no locality, 1F, BMNH; Santarem, 4M, 4F, ICCM. *São Paulo*: Avanhand (Garbe L.)*, 1F, MZSP.

Cicindela (Cylindera) marquardti Horn
Figs. 118, 125, 132, 141, 142, 150, 151, 156

Cicindela marquardti Horn, 1906: 91 (SYNTYPES, 4 males and 2 females in the IPZE bearing the following labels: "Staudinger Matto Grosso oder São Paulo/Type ! coll. W. Horn/ syntypus" (black letters on red label); TYPE LOCALITY, São Paulo int. aut Matto Grosso); 1915: 28,29,404; 1924: 48; 1926b: 77; 1938: 52.–Blackwelder, 1944: 18.–Rivalier, 1954: 265.

Recognition.— Diagnostic characteristics which distinguish adults of *C. marquardti* from those of other Brazilian species are the combination of the greenish head and pronotum contrasting with dark brown to black dull elytra, complete and broad apical and humeral lunules (Figs. 132a, b), sparse appressed setae on lateral portions of abdominal sterna 3,4,5 and several lateral setae on 2 and 6, and female and male genitalia as shown in Figures 141, 142,150,151.

Description.—

Body length. 7.5-8.0 mm M, *ca* 8.5 mm F.

Body colour. Head and pronotum are rugose with dark brown ground colour and bright green (mainly) and coppery reflections. Elytra dull, velvety, dark brown with hint of purple. Pleuron and venter glossy, testaceous to dark brown with faint metallic reflections. Proepisternum coppery or coppery-green.

Body setae. Proepisternum moderately setose. Dense appressed setae on ventral 0.33 of mesepisternum, mesepimeron, metepimeron and lateral 0.33 of mesosternum. Sparse appressed setae on lateral portions of abdominal sterna 3, 4, 5, and 2 and 6 with several setae only.

Other external features. Tooth of mentum short and sharply pointed. Labrum convex, elongate, five dentate (three prominent anterior, two small lateral), and six marginal setae (four anterior, two lateral) (Figs. 118a, b). Pronotum short, convex widened at anterior end, sutures deep (Figs. 125a, b). Coupling sulcus of mesepisternum of female a groove with deepened middle portion. Apex of front and middle trochanters with one sensory seta. Elytra with apices recurved in females, apical spine small. Humeral and apical lunules broad and complete, middle and marginal bands absent. Punctation shallow, obscure, green, broader punctures near shoulder and median suture (Figs. 132a, b). A few fine setae near shoulder and median

suture.

Female genitalia. Sternum 8 with narrow, deep V-shaped emargination in the apical end, apices each with two or three stout setae (Figs. 141a, 142a). Second gonocoxa with setae along medial margin (Figs. 141a, 142a). Second gonapophyses elongate with medial portion slightly shorter than the lateral portion (Figs. 141a, 142a). Syntergum 9 and 10 as in Figures 141b, 142b. Ventral sclerite in two parts with setae on lateral margins and anterior ends (Figs. 141c, 142c,d). Oviduct sclerite shield-shaped, or square (Figs. 141c, 142c). Bursa copulatrix with ventral sac on right (Figs. 141c, 142c,d). Spermatheca and duct approximately 2.0-3.0 mm.

Male genitalia. Median lobe stout with short tapered apex (Figs. 150a,c, 151a-c). Internal sac with flagellum 1.5 loops at base. Tooth dark elongate field. Arciform piece large. Central plate lightly sclerotized. Stylet large. Right bar and small stiffening rib well developed. Two or three apical finger-like brushes and small dark sclerite in right-ventral side of sac (Figs. 151a, d, e).

Geographical Variation.— Geographical patterns of variation have not been determined because few specimens of *C. marquardti* have been studied. The pattern of elytral maculations and sclerites of the female genitalia show limited intrapopulation variation.

Relationships.— *Cicindela marquardti* and *C. morio* are sister species.

Habitat and Period of Activity.— Adults have been collected beside rivers in January.

Geographical Distribution, Localities, Examined Specimens.— The total range of *C. marquardti* is restricted to a small area in Matto Grosso, Brazil (Fig. 156).

Brazil. *Matto Grosso*: no locality, 4M, 2F, IPZE; Trãs Lagoas, 1M, 6F, MZSP; Vacaria, 6M, 4F, MZSP.

The *friedenreichi* group

Adults of this group are characterized by reduced and partially depressed pale elytral maculations, and elongate apex of the median lobe. The group has three species, all of which are found in Brazil, *C. piligera*, *C. obsoletesignata* and *C. friedenreichi*. The geographical range of the *friedenreichi* group is centered in southeastern Brazil and extends westward to Ecuador. The *friedenreichi* and *morio* groups are sisters.

Cicindela (Cylindera) piligera Horn
Figs. 119, 126, 133, 143, 144, 152, 157

Cicindela piligera Horn, 1897b: 18 (TYPE LOCALITY, Minas Geraes); 1915: 406; 1926a: 307; 1938: 52.– Blackwelder, 1944: 19.– Rivalier, 1954: 265.

Recognition.— The character state combination of elongate labrum with seven uneven marginal teeth, elytra with maculations reduced to three depressed spots and large depression in basal 0.33, and a membranous sac on the ventral right side of the bursa copulatrix, together are diagnostic of *C. piligera*.

Synonyms and Types.— An examination of the holotype (IPZE) served to establish the name of this rare species.

Description.—

Body length. 7.5 mm M, 7.0-7.5 mm F.

Body colour. Dorsum slightly glossy, pleuron and venter glossy. Ground colour black; dorsum with slight coppery (mainly) and green reflections; pleuron and venter with coppery, green, and blue reflections.

Body setae. Lateral margins of the elytra, pleuron including ventral 0.5 of proepisternum and ventral end of mesepisternum, and lateral portions of metasternum, metacoxa, and abdominal sterna 1-6 (males) and 1-5 (females), setose.

Other external features. Labrum elongate seven dentate (not well defined in some specimens) with six marginal setae (Figs. 119a, b). Pronotum widest in middle sutures moderately deep (Figs. 126a, b). Coupling sulcus of mesepisternum of female a groove with central pit. Apex of front and middle trochanters with one seta. Elytra with recurved apices, apical spine small. Maculations reduced to three depressed spots. Punctures large green, row or large punctate depressions along median suture, large depression in basal 0.33 (Figs. 133a, b). Microsculpture isodiametric, bead-like.

Female genitalia. Sternum 8 with moderately deep and narrow apical emargination, apices narrow, each with three long stout setae (Figs. 143a, 144a). Second gonocoxa with a few setae along medial margin (Figs. 143a, 144a). Second gonapophyses and syntergum 9 and 10 as in Figures 143a, b, 144a, b. Bursa with sac on ventral right side (Figs. 143c, 144c). Ventral sclerite with posterior emargination and lateral projections, setose apical extension on right dorsal side (Figs. 143c, d, 144c). Oviduct sclerite shield-like (Figs. 143c, 144c). Spermatheca duct fused to bursa at base, spermatheca duct at least 1.25 mm (broken in dissection).

Male genitalia. Cicindela piligera type; median lobe as in Figures 152a-c. Flagellum 1.5 loops at base (Fig. 152e). Stylet, arciform piece, right bar, small stiffening rib and central plate all well developed (Figs. 152d, e).

Geographical Variation.— Insufficient material for analysis.

Relationships.— *Cicindela piligera* and *C. obsoletesignata* are sister species.

Habitat and Period of Activity.— Unknown.

Geographical Distribution, Localities, Examined Specimens.— Two adults have been collected in Minas Gerais, Brazil and one in Ecuador (Fig. 157).

Brazil. no locality, 1F, IPZE. *Minas Gerais*: no locality, 1M (holotype), 1F, IPZE.
Ecuador. No locality, 1F, BMNH.

Cicindela (Cylindera) obsoletesignata Horn
Figs. 120, 127, 134, 145, 153, 157

Cicindela obsoletesignata Horn, 1895b: 91 (TYPE LOCALITY, St. Catharina); 1896c: 169; 1915: 406; 1926a: 307; 1938: 52. –Blackwelder, 1944: 19.– Rivalier, 1954: 263.– Vidal Sarmiento, 1966b: 31.– Sumlin 1979: 105.

Recognition.— The character state combination of the black body; unidentate labrum, dark at the base, with six almost marginal setae (seven in a few specimens) (Fig. 120); sparse and fine body setae; and depressed obsolete maculations of the elytra (Fig. 134) distinguishes adults of *C. obsoletesignata* from those of other Brazilian species of *Cicindela*.

Synonyms and Types.— The name *C. obsoletesignata* is based upon an examination of the holotype and three females and one male determined by Horn.

Description.—

Body length. 6.0 mm M, 7.0-7.5 mm F.

Body colour. Body with dull to slightly glossy dorsum and slightly glossy venter; black, with black to rufopiceus venter of abdomen, genae with metallic reflections in some specimens, a hint of metallic reflection from dorsum and venter.

Body setae. Fine sparse setae on pleuron and sterna 1-5 (female) and 1-6 (male) of abdomen.

Other external features. Labrum unidentate, with 6 almost marginal setae (Fig. 120). Pronotum slightly wider anteriorly, sutures shallow (Fig. 127). Coupling sulcus of mesepisternum of female a distinct dorso-ventral groove. Apex of front trochanters each with one seta, middle trochanters glabrous. Elytra with

apices slightly recurved or not, apical spine tiny or obsolete; maculations depressed with effaced or obsolete middle band and apical lunule; punctures shallow, green; row of large markedly depressed punctures near median suture and shoulder (Fig. 134).

Female genitalia. Sternum 8 with wide and moderately deep apical emargination; apices each with three short stout setae (Fig. 145a). Second gonocoxa with grooves in medial margin (Fig. 145a). Second gonapophyses as in Figure 145a. Syntergum 9 and 10 rectangular (Fig. 145b), bursa with larged wrinkled and folded membranous sac with darkened area (Figs. 145c-f). Ventral sclerite wide, with a posterior emargination and lateral projections; right dorsal apical extension of ventral sclerite setose (Figs. 145c-f). Oviduct sclerite shield-like (Fig. 145c), spermatheca and duct lost in dissection.

Male genitalia. Median lobe and internal sac *C. obsoletesignata* type (Figs. 153a-e); flagellum 1.5 loops at base (Figs. 153d, e). Stylet prominent (Figs. 153d, e). Arciform piece, right bar, small stiffening rib, and central plate present (Figs. 153d, e).

Geographical Variation.— An adequate number of specimens was not available for the determination of patterns of geographic variation.

Relationships.— *Cicindela obsoletesignata* and *C. piligera* are sister species.

Habitat and Period of Activity.— Unknown.

Geographical Distribution, Localities, Examined Specimens.— Figure 157.
Argentina. *Chaco*: no locality, 1F, IPZE.
Brazil. *Santa Catarina*: no locality, 1M, 3F (including type), IPZE.

Cicindela (Cylindera) friedenreichi Dokhtouroff
Figs. 121, 128, 135, 146, 154, 157

Cicindela friedenreichi Dokhtouroff, 1887: 154 (TYPE LOCALITY, Sta. Cathari .– Horn, 1904: 87; 1915: 407; 1926a: 309; 1938: 52. –Blackwelder, 1944: 18.– Rivalier, 1954: 263.– ꓼ andl, 1963: 578.

Recognition.— The character state combination of the unidentate labrum with seven or eight setae close to the anterior margin (Figs. 121a, b), dark body, and elytra with a humeral spot, complete and broad apical lunule, elongate and depressed middle band (Figs. 135a, b), and a row of very large depressed punctures along the median suture distinguishes adults of *C. friedenreichi.*

Synonyms and Types.— The name is based upon comparison of the original description with specimens on loan from R.R. Murray.

Description.—
Body length. 7.5 mm M, 7.5-8.0 mm F.
Body colour. Dark, almost black with coppery and green reflections, dorsum slightly glossy, venter glossy.
Body setae. Appressed setae sparse to moderate in anterior 0.5 and lateral portions of pronotum, pleuron (mesepisternum glabrous mainly), lateral portions of metasternum and metacoxa, and lateral portions of abdominal sterna 1-6 (sternum 6 of female with a few setae).
Other external features. Labrum convex, unidentate with seven or eight setae very close to margin (Figs. 121a, b). Pronotum widest in anterior 0.5, sutures deep in front and hind angles (Figs. 128a, b). Coupling sulcus of mesepisternum of female a long sinuate groove. Front trochanters with one sensory seta. Elytra with apical end tapered, slightly recurved in females, to small apical spine, maculations variable as in Figures 135a, b, with humeral spot and complete apical lunule, apical 0.5 of middle band elongate and depressed, distinct row of large depressed blue-green punctures near median suture and shoulder, punctation shallow and green, microsculpture isodiametric bead-like.
Female genitalia. Sternum 8 with deep V-shaped apical emargination, apices each with three stout setae (Fig. 146a). Second gonocoxa with grooves on median margin, second gonapophyses as in Figure 146a. Syntergum 9 and 10 as in Figure 146b. Ventral sclerite with a pair of setose anterior lobes, anvil-shaped (Figs. 146a-e). Spermatheca and duct lost in dissection.

Table 1. Classification of characters used in the construction of a genealogy of the Brazilian species of *Cicindela*

No.	Character	Character State	
		Plesiomorphous	Apomorphous
1	Body size	Average (7.0-8.0 mm)	Large (>8.0 mm) A Small (<7.0 mm) A[1]
2	Head and pronotum: colour	Dark brown to black with some metallic reflections	Bright coppery (with green in some specimens) B Metallic green or blue B[1]
3	Head and pronotum: rugosity	Shallow	Deep C
4	Rugosity between eyes	Shallow, no swirls	Two shallow pits (swirls of rugosity) D Deep D[1]
5	Proepisternum punctuation	Shallow, random	Deep, few, evenly distributed E
6	Elytra surface	Dull	Matte, velvety F Slightly glossy F[1] Glossy F[2]
7	Elytra: ground colour	Dark brown to black with faint metallic reflections	Metallic reflections (coppery and green), brighter G Faintly purple G[1]
8	Frons: setae	Absent	Present H Dense appressed H[1]
9	Clypeus: setae	Absent	Present I Dense appressed I[1]
10	Genae: setae	Absent	Present J Dense appressed J[1]
11	Proepisternum: setae	Sparse	Moderate K Dense K[1] Dense appressed K[2] Absent K[3]
12	Mesepisternum: setae	Sparse	Moderate L Dense L[1] Dense appressed L[2] Glabrous L[3]

Table   1   (continued)

No.	Character	Character State	
		Plesiomorphous	Apomorphous
13	Middle of abdominal sterna: setae	Absent	Present M Few additional erect M[1]
14	Setose lateral portions of abdominal sterna	1–6	1–5 N 2-6 N[1] 3–6 sparse N[2] 1–3 N[3]
15	Labrum: width	Average	Narrow O Elongate centre O[1] Elongate O[2]
16	Labrum: margin	Unidentate	Edentate P Tridentate P[1] 5-Dentate P[2] 7-Dentate P[3] >7-Dentate P[4]
17	Labrum: setae position	Submarginal	Nearer to margin (some or all setae) Q Marginal Q[1]
18	Labrum: setae	8 (average)	<8 (average) R >8 (average) R[1]
19	Mentum tooth: length	Average	Short S Long S[1]
20	Antenna segments: colour	Normal	5–6 pale T 5–11 pale T[1]
21	Pronotum: width	Average	Narrow U Broad U[1]
22	Coupling sulcus: shape	Groove (di nct)	Groove with deeper centre V Groove with central pit V[1] Pit V[2] Almost absent V[3]
23	Middle trochanter: setae	Absent	Present W
24	Abdominal sternum 5 of ♀: unpigmented bell-shaped spot	Absent	Present X

Table 1 (continued)

No.	Character	Character State	
		Plesiomorphous	Apomorphous
25	Elytra: pale markings	Narrow to broad, complete or almost complete	Reduced Y
			Reduced and partially depressed Y^1
			Effaced Y^2
			Broad and fused Y^3
			Broad, fused, ragged, spotted Y^4
			Ragged Y^5
			Narrow, fused, partly ragged and spotted Y^6
26	Elytra: foveae	Obvious near shoulder and median suture	Not obvious Z
			Few Z^1
			Absent Z^2
			Very large Z^3
27	Abdominal sternum 8 ♀: apical emargination	Broad, average depth	Broad, deep a
			Broad, shallow a^1
			Very broad, deep a^2
			Very broad, shallow a^3
			Narrow, deep a^4
28	Abdominal sternum 8 ♀: stout apical setae size	Average length	Short b
			Long b^1
29	Abdominal sternum 8 ♀: stout apical setae number	2–3	4 c
			5 c^1
			>5 c^2
30	Ventral sclerite: shape	Broad, tapered posteriorly	With median ridge d
			Two elongate posterior projections d^1
			Two anterior lobes and two posterior projections d^2
31	Ventral sclerite: setae	Absent	Present e
32	Oviduct sclerite: form	Shield-shaped	Rectangular, not laterally broadened f
			Narrow f^1
			Membranous f^2

Table   1   (continued)

No.	Character	Character State	
		Plesiomorphous	Apomorphous
33	Spermatheca and duct: length	1.0–1.5 mm	1.5–2.5 mm g >2.5 mm g[1]
34	Bursa copulatrix: setae	Absent	Present h
35	Bursa copulatrix: shape	Normal	One ventral right out-pocketing i Two anterior lateral out-pocketings i[1]
36	Median lobe: apex	Short	Short, ventral notch j Hooked ventrally j[1] Elongate j[2] Bent dorsally j[3]
37	Flagellum	Present	Absent k Fewer than 1 1/2 coils (loops) at base k[1]
38	Tooth: condition	Sclerotized	Membranous 1
39	Tooth: shape	Elongate	Elongate with spatulate apex m Short m[1] Elongate arising from two long thin roots of equal length m[2]
40	Internal sac: two finger-like darkened fields, one spatulate-like	Absent	Present n
41	Arciform piece: shape	Narrow	Broad o Very broad tapered apically o[1]
42	Arciform piece: position	Oblique	Longitudinal p
43	Central plate	Not joined to shield	Joined to shield q Absent q[1]
44	Shield	Present	Absent r

Table   1   (continued)

No.	Character	Character State	
		Plesiomorphous	Apomorphous
45	Shield: shape	Single apex	Single apex tapered s
			Single apex rounded s[1]
			Single apex rounded, bent s[2]
			Single apex tridentate s[3]
			Two apices s[4]
			Two apices short, blunt, s[5]
			Heart-shaped two apical lobes s[6]
			Two apices elongate s[7]
			Two apices long filamentous s[8]
			Two apices, one a prominent round lobe s[9]
			Two apices, round lobe, short spine s[10]
			Three apical lobes s[11]
			Folded laminate s[12]
			Folded laminate leaf-like s[13]
			Reduced s[14]
46	Small stiffening rib	Present	Absent t
47	Stylet	Present	Absent u
48	Stylet: form	Average length to long	Short v
			Bifid v[1]
			Broad v[2]
49	Sagittal sclerotized plates	Absent	One present w
			Two present w[1]
50	Cuña (triangular piece)	Absent	Short x
			Long x[1]

Table 2. Selected characters of South American, Central American and Caribbean species of the Subgenera *Brasiella, Gaymara*, *Plectographa* and *Cylindera**.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14 +	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
cubana ⊙	.A^1	BB^1	.	D^1			.G			J			M		O^2	.									Y	Z^3																								
acuniai	A^1	B^1	.	.	.	.F^2	.G	.	.	.	.	L^3	M	N^3	.	.	.	R	.	.	.		.		Y	Z^3	a								i															
viridicollis	.	B^1	.	.	.	.F^1	.G	.	.	.	.	.	M	.	.	.	.	.R	.	.	.	V^1	.	.	.Y	Z^2										j^1	k	.	.	.	.	p	q^1	.	s^1	t	.	.v^2	.	.
wickhami	.A^1	BB^1	.	.	.	FF^1	G	.	.	.	.	.	M	.	.	.P	.	R	.	.	U	V^1	.	X	Y	ZZ^1										j^1	k	.	.	.	.	p	q^1	.	s^9	t	.	.v^2	.	.
mendicula ⊙	.	.	.	.	.	.	.	.	.	.	K^3	L^3			.	P	.	.		.	U		.		Y											j^1	k	.	m^2	.	.	p	q^1	.	s^2	t	.	.v^2	.	.
sphaerodera ⊙	.	.	.	.	.	.	.	.	.	.	K^3	L^3	.		O	P	.	.		.	U^1		.		Y											j^1	k	.	m^2	.	.	p	q^1	.	.	.	.	.v^2	.	.
hemichrysea ⊙	.	B	.	.	.	.	.	.	.	.	K^3				.		.	.R^1		.	U		.		Y											j^1	k	.	.	.	.	p	q^1	.	s	t	.	.v^2	.	.
argentata ø	.A^1	.	.	.	.	.	.	.	.	.	.	.	M	.	.	P^1	.	.	.	.	U	V^1	.	X	.Y	Z	a	b	.	.	.	f^2	.	.	.	j^1	k	.	m^1	.	.	p	q^1	.	s^4	t	.	.	.	.
venustula ⊙	.	.	.	.	.	.	.	.	.	.	.				.		.	.		.	U^1				Y	Z										j^1	k	.	.	.	.	p	q^1	.	s^4	.	.	.v^2	.	.
obscurella ø	.A	.	.	.	.	.	.	.	.	.	.	.	M	.	O^2	P	.	.	.	.	U	.	.	X	Y	Z	a	b	c	d	.	f^2	.	h	.	j^1	k	.	.	.	.	p	q^1	.	.s^4	t	.	.	.	.
pretiosa ø	.A	.	.	.	.	.	.	.	.	.	.	.	.	.	O^1	P	.	.	.	.	.	.	.	.	Y	Z	a	b	.	.	.	f^2	.	h	.	j^1	k	.	.	.	.	p	q^1	.	s^4	t	.	.	.	.
rivalieri ⊙	A^1	.B	.	.	.	.	G	.	.	.	.		M	.	O	P	.	.		.	U				Y	.										j^1	k	.	.	.	.	p	q^1	.	s^{11}		.	.v^2	.	.
amaenula ø	.	B	.	.	.	F^1	G	.	.	.	.	.	M	.	.	P^1	.	.	.	.	.	.	.	X	.	Z	a^1	.b	c	.	.	f^2	.	h	.	j^1	k	.	m^1	.	.	p	q^1	.	s^6	.	.	.	.	.
aureola ø	A	B	.	.	.	.	G	.	.	.	.	.	M	.	.	P	.	.	.	.	.	.	.	X	YY^2	Z	a^1	b	.	.	.	f^2	.	h	.	j^1	k		.	.	.	p	q^1	.	s^6	.	.	.	.	.
horioni ⊙	.	B^1	.	.		.	GG^1	.	.	.					.	P	.	R			U^1				Y	Z																								
dolosulaffinis ⊙	.	.	.	.	.	.	.									.P^1									.	Z										j^1	k	.	.	.	.	p	q^1	.	s^3	.	.	.	w	.
tippmanni ⊙																P^1									.	Z										j^1	k	.	.	.	.	p	q^1	.	s	.	.	.	w	.
dolosula ø	.	.	.	.	.	.	.	.	.	.	.	.	M	.	.	P^1	.	.	.	.	U		.		.	Z										^{x}j^1	k	.	.	.	o^1	p	q^1	.	s^5	t	.	.	w^1	.
misella ø	A^1	.	.	.	.	.	.	.	.	.	.	.	M	.	O	P^1	.	.	.	.	U	V^2	.	.	.	Z	a^1	b	.cc^1	.	.	f^1	.	.	.	j^1	k	.	.	.	o^1	p	q^1	.	s^8	t	.	.	w^1	.
zuelensis ⊙	.	.	.	.	.	.	.	.	.	.			M		O	.	.	R		.	U		.		.	Z										j^1	k	.	.	.	.	p	q^1	.	s^7	t	.	.	w	.
stamatovi ⊙	A^1	B	.	.	.	F^1	G	.	.	.	.	.	.	.	.	.	.	.			.				.																									
hamulipenis ø	A^1	.	.	.	.	.	.	.	.	.	K	L	M	.	O^2	.	.Q	R	.	.	.		.		Y^2	Z^1										j^1	k	.	m^1	.	.	.	q^1	.	s^7	t	.	.	.	.
brevipalpus ø	A^1	.	.	.	.	.	.	.	.	.	K	.	M	N^2	O^2	.P^2	.Q	R	.	.	U		.		Y^2	Z^2										.	k	.	m^1	.	.	.	q^1	.	s^4	.	.	.	.	.
banghaasi ø	.A^1	.	.	.	.	.	.	H	I	J	K	L	M	.	O^2	.	.	.	.	.	.	V^2	.	.	.	.	.	.	cc^1	d	.	f^2	.	.	.	j^1	k	.	m^1	.	.	.	q^1	.	s^3	t	.	.	.	.
minarum ø	.A	.	.	.	.	.	.	.	.	.	.	.	M	.	O	.	.	.	.	.	.	V^1	.	-	Y	Z^2	.	b	.	d	.	f^2	-	.	.	j^2	k	.	m^1	.	o	.	q^1	.	.	.	.	.	.	.
nebulosa ⊙	.A	.B	.	.	.	F	.G	.	.	.	.	.	M	.	O	.	.	.R^1	.	.	.U		.		Y	Z^2										j^1	k	.	m^1	.	.	.	q^1	.	s^{10}	t	.	.	.	.
mandli	.	.	.	.	.	.F	.	.	.	.	.	.	M	$\overset{N}{.}$	O	.	.	.	.	.	U	V^1	.	X	Y	Z^2										j^1	k	.	m^1	.	.	.	q^1	.	.	t	.	v	.	.
insularis	.	.	.	.	.	.F	.	.	.	.	.	.	M	$\overset{N}{.}$	O	.	.	.	.	.	U	V^1	.	X	Y	Z^2										j^1	k	.	m^1	.	.	.	q^1	.	.	t	.	.	.	.
balzani	.A	.	.	.	.	.	G	.	.	J	K	L	.	.N	.	P^1	Q	R	.	.	.	.	.			Z^2	.	b^1	.	d^1	.	f^2	.	.	.	j^3	k	l	.	.	o	.	q^1	.	s^{15}	t	.	.	.	.
chlorosticta ø	.A	B	C	D	.	.F	G	.	.	.	.	.	.	$\overset{N}{.}$	O^2	P^1	.	R	.	.	U^1	.	.	.	.	Z^3	a^1	.	c	d^1	e	f	.	.	.	j	k	l	.	n	o	.	q	.	.	t	.	v	.	.
staudingeria ø	A	B	C	D	.	.F	G	.	.	.	.	.	.	$\overset{N}{.}$	O^2	P^1	.	R	.	.	U^1	.	.	.	.	Z^3	a^1	b^1	c^1	d^1	e	.	.	.	.	j	k	l	.	n	.	.	q	.	.	t	.	v	.	.
nigroreticulata ø	A	B	C	D	.	F	G	.	.	.	.	.	.	.	.O^2	.P^1	.	R	S^1	.	U^1	V	.	.	.	Z^3	a^1	b	cc^{1,2}	d^1	e	.	.	.	.	j	k	l	.	n	.	.	q	.	s	t	.	v	.	.
paranigroreticulata ø	.A	.	C	D	.	.	.	H	I	J	K	L	.	.	O^2	P^1	.	R	S^1	.	U^1	V	.	.	Y	Z^3	a^1	b	c^1	d^1	e	.	g	.	.	j	k	l	.	n	.	.	q	.	.	t	.	v	.	.
anulipes ø	.	.	.	.	E	F	.	.	.	.	K	L	.	.	O^2	P^1	Q	R	S^1	.	.	.	.	.	Y	Z^2	.	b^1	c^1	d^1	.	.	.	.	.	j^2	k	l	.	.	o	.	q	.	.	t	.	v^1	.	.

(continued on next page)

Table 2 (continued)

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
halophila	.A	B				F^2	G	.H	J	K^2			.N					R			V^2	W			y^3		a^3	b^1	c^2	d^2		g^1		h				m^2				q^1			s^{12}					x^1
sicsalicicola	A	B				F^2	G	H	I	K^1	.M^1.N							R	s^1		.U^1	v^3			y^3	z		.b^1	c^2	d^1		g^1								o					s^{12}		v			xx^1
sinuosa	A	B				F^2	G			K^2	.H^1										U^1				y^3	z^2		.b^1	c^2	d^1		g^1	h					E				q^1			s^{12}					x
suturalis Ø	.AA^1	B				$F^{1.2}$G				K^2 L^2				.0^2											y^3	z^2	a						i													s^{12}					
hirsutifrons ⊙	A	B				F^1 G	H^1	T^1	J^1	K^2 L^2	M	.0		0^2				R			U^1				y^4	z				d^1								E							s^{12}		u			x^1
nivea Ø	A	B				F^1 G	H^1	T^1	J^1	K^2 L^2	.M		.N	0^2					s^1		U^1				y^4	z^2	a^1	b^1	c^2	d^1		g^1						E				q^1			s^{12}		u			x^1
ramosa	A	B				F^1 G	H^1	T^1	J^1	K^2				0					s^1		U^1	V^3.W			y^4	z^1	a^3			d^1		g^1						E				q^1			s^{12}		u			x^1
nahuelbutae	A	.B				F^1 G	H^1	T^1	J^1 .KK^2	L^2 K^2		M^1.N					.R^1	s^1		.U^1				y^4	z^1													E		o		q^1			s^{12}					x^1
mixtula	.A					F^1 G	H	I	J	K^2							.R	s^1		.U^1	.v			y^5	z^2	a^1	b^1	c	d^1		g^1						E				q^1			s^{13}		v			x
ritsemai	.A					F^1 G	H	I	J.K						.0		R	s^1		U^1	.v			.$y^{4,6}$	z^3	a^1		cc^1	d^1		g^1						E		o		q^1			s^{12}		v^2			x^1
drakei	.A						H	I	J.K.L			.N		0^2			.R^1	s^1		U^1	.v			.$y^{4,6}$	z^3		b		d^1	e	g^1						E				q^1			s^{12}		v			x^1
melaleuca Ø	A					F^2	H	I	J.K.L			.N		0^2				s^1		U^1				y^4	z^3			cc	d^1	d^2 e	g^1					E^1							s^{12}		u			x^1
patagonica Ø	A						H	I	J.K			N		0			.R^1	s^1		U^1.W				y^5	z^3	a	.b	c	d^1		g^1						E		o		q^1			s^{12}		u			x^1
gormazi	A						H	I	J.K		.M.N			0			.R^1	s^1		U^1 V.W				.y^5	z^3		b	c	d^1		g					k^1		E		o		q^1			s^{12}		v			x^1
chiliensis	.A						H		J					0^2	P^1		.R^1			U^1 V.W				.y^5	z^2	a	b	c^1	d^1		g				f^1						q^1			s^{12}		u			x^1
nigrovittata Ø	.A		C	D		F	H					N		0^2			R	s^1		.U^1	v^3			y	z	a	b	c^1	d^1		g										q^1			s^{14}		-			x
eugeni ⊙	.A						H																		.y^4	z^1				d^1						j								r						x
apiata Ø	.A														0		.R^1										a^3					g												r	s^{14}					x
kollari Ø	.A^1	B				F^1			J	K^1			.N		.0		R	T^1		U^1	W			y^3	z^1	a^3	b	c^1	d^2 e		g			j^2	1								r						
malaris ⊙	.A^1					F^1			J	K^1					P		.P	.U^1	U^1		W			y^3	z^2	a^3			d^1		g			j^2															
confluentesigmata Ø	A					F^1			J	K.L				0^2	P^3.0	R	R	T^1		U^1	W			y^3	z^1	a^4	cc^1	d^2 e	f			f^1	j^3	j^3	1								r	-				x
granulipennis ⊙	A								J					0^2	P^4.q^1		.R^1		.U					y																									
morio Ø	.AA^1					.F				K.L		.N		0^2	P^4.q^2		.R^1			U^1	W			$y^{2,3}$	z^1	a	b		d^2 e		g	g^1		i		1					q^1	r				v			
marquardti	.A	C				.F.c^1				K.L^1		N^1		0^2	P^3.q^1	R	.R			.U^1 V.W				.y	z^1	a	b		d^2 e		g	g^1		i	j^2	1					q^1	r				v			
ptiligera Ø						F^1				K.L		.N			P^2.0	R	.R			U^1 V.W				y^1	z^1	a^2	b		d^2 e		g			i	j^2						r					v^1			
obsoletesigmata Ø	.A^1					.F^1				K.L		.N		0^2	.q		R			U^1				y^1	z^3	a^2	b		d^2 e		g			i	j^2						r					-			
friedenreichi	.A^1					.F				K.L		.N		0^2	.q		R			U^1				y^1	z^3				d^1		g											r					-			

* Letters, apotypic characters from Table 1; ', plesiotypic characters; capital letters denote genitalic characters; lower case letters denote non-genitalic characters; capital letters denote genitalic characters; letters and points side by side denote both plesiotypic and apotypic characters occur in the same species; dashes and blanks denote absent or undetermined characters respectively.
+ Top and bottom letters or points indicate female and male respectively shown for Brazilian species
⊙ Species not seen by us.
Ø Brazilian species.
× Small dentiform projection.

Male genitalia. Median lobe with elongate and tapered apex (Figs. 154a-c). Internal sac with flagellum 1.5 loops at base. Tooth and stylet well developed. Arciform piece, right bar, small stiffening rib and central plate well developed, additional stout sclerite between small stiffening rib and right bar (Figs. 154d, e).

Geographical Variation.— Insufficient material was available to determine patterns of geographical variation; variable characters appear to be mainly body colour ranging from greenish to black through coppery, and the maculations of the elytra.

Relationships.— *Cicindela friedenreichi* is sister to the lineage that gave rise to sister species *C. piligera* and *C. obsoletesignata*.

Habitat and Period of Activity.— Unknown.

Geographical Distribution, Localities, Examined Specimens.—
Southern Brazil, Rio Grande do Sul, Santa Catarina (Fig. 157).
Brazil. *Rio Grande do Sul*. Torres, 1M, 6F, RRMC.

HISTORY OF SOUTH AMERICAN SPECIES OF SUBGENERA *BRASIELLA, GAYMARA, PLECTOGRAPHA* AND *CYLINDERA*

Introduction

Organisms are wards of their history. Each taxon embodies an evolutionary heritage based on a special kind of ancestry. In time this legacy is altered with acquired genetic and biogeographical attributes which are carried to descendants. Natural classifications reflect these processes as part of the main course of organismic history. They present branching lineages and heritage changes in a dichotomous phylogenetic framework.

In the phylogeny section that follows reconstructed phylogenies are based on methods and philosophy of Hennig (1966). Phylogenetic relationships are inferred from determinations of apomorphous (derived) and plesiomorphous (ancestral) characters of adult beetles from which the reconstructed genealogies are expressed. Biogeographic considerations, based on the reconstructed phylogenies, attempt to deduce distributions of species and species groups.

Brazilian and related South American taxa of *Cicindela* were included, which together appeared to form monophyletic assemblages largely within South America. We examined adult specimens of 29 Brazilian and 16 non-Brazilian species. In addition the genitalia of males and females were dissected and their characteristics documented for each of 29 and 26 Brazilian species and 10 and 11 non-Brazilian species respectively. Data for 16 non-Brazilian species not examined by us were obtained from original descriptions, writings and figures in Horn (1915, 1938), Rivalier (1954, 1955), Mandl (1963, 1973), Vidal Sarmiento (1966a,b, 1967), Peña (1969), Peña and Barria (1973), and Sumlin (1979).

Phylogeny

The purposes of this section are to postulate phylogenetic relationships of sister groups and to classify them. Detailed accounts and viewpoints of the method of phylogenetic reconstructions can be obtained from Hennig (1966), Ross (1974),

Eldredge and Cracraft (1980), Wiley (1981), Charig (1982), Maynard Smith (1982), and Patterson (1982).

Phylogenies are deduced in two steps. First character states are determined to be apomorphous or plesiomorphous. Second, sister groups are established from synapomorphous (shared apomorphous) character states. It is not always easy to decide the direction of a character state trend in a group (*in-group* comparison) or whether a character state is apomorphous or plesiomorphous. By comparing character states of a group with those of related groups (*out-group* comparison) usually one can decide reasonably which is apomorphous and which plesiomorphous.

Plesiomorphous and apomorphous character states of Brazilian species of *Cicindela* are postulated in Tables 1, 2 and 3, and used as the basis for the construction of phylogenetic diagrams (trees, cladograms) given in Figures 158-163. In Table 1 each character is described and numbered. Apomorphous states of non-genitalic characters are assigned a capital letter and those of genitalic characters a lower case letter. Superscript numbers placed beside the letters indicate one of two or more apomorphous states of a character, and a series of numbers indicates a morphocline. In Table 2, points and letters or numbered letters indicate plesiomorphous and apomorphous character states respectively.

Decisions about plesiomorphy and apomorphy given below are based on generalized out-group comparisons of character states among North and South American species groups or subgenera of the genus *Cicindela*. As an operational rule for out-group comparisons we followed that of Watrous and Wheeler (1981) which states that for a given character with two or more states within a group, the state occurring in related groups is assumed to be the plesiomorphous state. Thus the word common as it is used here refers to the high frequency of a plesiomorphous character state among species groups or subgenera.

Body size (1). Average size plesiotypic though arbitrarily viewed, is found in most species groups.

Head and pronotum: colour (2) and rugosity (3). Dark brown or black with shallow rugosity is very common and deemed plesiomorphous.

Rugosity between eyes (4). Two deep rugose pits are found only in four species: apomorphous.

Proepisternum: punctuation (5). Deep widely spaced punctures present in *C. anulipes* only: apomorphous.

Elytra: surface (6) and ground colour (7). A dull and dark brown or black combination is plesiomorphous being the most common condition among groups.

Setae on frons (8) clypeus (9) genae (10). Absence of setae is the condition of the majority of species groups: plesiomorphous.

Setae on proepisternum (11) and mesepisternum (12). Density of setae tends to be a gradient condition, though the distinctly sparse state appears to be widespread: plesiomorphous.

Setae on middle of abdomen (13). Absent is the plesiomorphous state.

Setae on lateral portions of abdominal sterna (14). Most species bear setae on sterna 1-6: plesiomorphous.

Labrum: width (15) and margin (16). The average width and unidentate states are widespread among species groups: plesiomorphous.

Labrum setae: position (17) and number (18). Most species have submarginal setae (plesiomorphous); an average number of eight setae is deemed plesiomorphic among species groups though fewer than 8 is common in Brazilian species.

Mentum tooth: length (19). Average length is the widespread state: plesiomorphous.

Antenna segments: colour (20). Lack of metallic reflections (pale) is uncommon: apomorphous.

Pronotum: width (21). Average width widespread though not uniformly so within species groups: plesiomorphous.

Coupling sulcus: shape (22). A distinct groove straight or slightly sinuate is found in the majority of species groups: plesiomorphous.

Middle trochanter: seta (23). Absent from most species: plesiomorphous.

Abdominal sternum 5 of female: unpigmented bell-shaped spot (24). Present in a few species, apomorphous.

Elytra: pale markings (25). Highly varied in detail though general features somewhat more stable; narrow to broad, complete or almost complete more prevalent than other combined conditions: plesiomorphous.

Elytra: foveae (26). Obvious though not large near suture and shoulder is plesiomorphous.

Abdominal sternum 8 of female: apical emargination (27). A somewhat varied character but stable within some species groups. Broad, average depth: plesiomorphous.

Abdominal sternum 8 of female: stout apical setae size (28) and number (29). Average length: plesiomorphous; 2-3 characteristic of most species: plesiomorphous.

Ventral sclerite: shape (30). Anterior and posterior projections and a median ridge are uncommon in most species groups of South America: apotypic; and a well defined median ridge is uncommon: apomorphous.

Ventral sclerite: setae (31). The absent state is widespread: plesiomorphous.

Oviduct sclerite: form (32). A shield shape is the common state: plesiomorphous.

Spermatheca and duct: length (33). A short (1.0-1.5 mm) spermatheca and duct is common: plesiomorphous.

Bursa copulatrix: setae (34) and shape (35). The presence of setae and outpocketings are states uncommon in South American species: apomorphous.

Median lobe: apex (36). A short unhooked apex is a widespread state and by out-group comparison considered to be plesiomorphous.

Flagellum (37). Absence of a flagellum is uncommon within *Cicindela* world-wide: apomorphous.

Tooth: condition (38) and shape (39). A sclerotized elongate tooth is common: plesiomorphous.

Internal sac: two finger-like darkened fields, one spatulate-like (40). These are apomorphous if present; found in a few species.

Arciform piece: shape (41) and position (42). The narrow and oblique states are common and therefore plesiomorphous.

Central plate (43). A central plate not joined to the shield appears to be common: plesiomorphous.

Shield (44) and (45). A distinct shield, and single apex both plesiomorphous.

Small stiffening rib (46). The present rib state is slightly more common than the absent one and thus deemed to be plesiomorphous.

Stylet (47) and form (48). An average to long stylet is common: plesiomorphous.

Two sagittal sclerotized plates (49). Rarely present: apomorphous.

Cuña (50). A small triangular sclerite near the dorsal side of the flagellum of the male, shown by Vidal Sarmiento (1966b) to occur in species of *Plectographa* and *Cylindera*: apomorphous.

Because of the large number of diverse characters used in the reconstructed phylogeny a strict hierarchical system of character weighting was diffic lt to establish. As a general rule we judged characters in demonstrating relation hips, from good, if stable and corroborating with other stable characters inter-specifically, to poor, if unstable intra-specifically. Characters of the male and female genitalia, morphometric features, loss of a good character, distribution of body setae, colour pattern of the elytra, and body colour, were generally but not consistently applied in descending order of value. For accounts of theory and methods of character weighting we refer the reader to Funk and Wheeler (1986), Neff (1986), and Wheeler (1986), and, in particular to how they relate to carabid beetles, to Ball and Nimmo (1983).

In the formation of a genealogy the largest groups of species that consistently share apomorphous character states are treated as evolutionary units. In our scheme they are a monophyletic complex of subgenera of *Cicindela* found primarily in South America. Four subgenera are recognized, the species of which are listed in Table 2.

The reconstructed phylogeny of the subgenus *Brasiella* (Fig. 158) is based on characters of 29 species listed in Table 2. Genitalic characters of males and females dissected by us were observed and documented for 11 species, and those of males only were determined from publications for 23 species. Genitalic characters were not determined for both sexes of four species, and for females of 14 species. Eight non-genitalic characters were not determined among 21 species.

Seven characters account for 12 evolutionary reversals and 44 characters for 122 parallelisms. Although 452 characters were not determined, one third of the full

potential character number 1450, we are confident that our reconstructed phylogeny of this subgenus will stand up to rigorous testing, as the system is based mainly on complex characters that frequently corroborate each other in various lineages.

The presence of setae (pubescence) on the middle of the abdominal sterna, short apical setae on abdominal sternum 8 and membranous oviduct sclerite of the female, and hooked apex of the aedeagus, absent flagellum and central plate of the male, characterize the original ancestral lineage of *Brasiella*.

The relative positions of species in the *viridicollis* group may require changing later on, because undocumented good characters are absent from this species group genealogy. However for now we treat *C. acuniai* and *C. viridicollis* as sister species on the basis of the bicolourous adult body, bright blue or green head and pronotum with brown to coppery elytra though we recognize that different relationships may be derived among species by differential weighting of B^1, F^1, R, Z^1 or Z^3, and when the genitalia of both sexes for the four species become known.

The *aureola* species group consists of *C. rivalieri*, *C. amaenula* and the sister species *C. aureola/C. horioni*. We have not seen adults of *C. horioni* and have placed this species mainly on the basis of the maculations of the elytra as drawn by Mandl (1956: 388). A bell-shaped unpigmented area of the hind margin of sternum 5 of females is present in the latter three species, and also in species of the *argentata* species group. This is an unusual character found in no other *Brasiella* species. Therefore, we are not comfortable with this separation of the *aureola* and *argentata* groups but it seems the most parsimonious at the moment.

In the *misella* group, the positions of *C. dolosulaffinis* and *C. tippmanni* are uncertain. We have put them together as sister species on the basis of general habitus. We have not seen specimens and many adult and genitalic characters have not been documented (Table 2).

The reconstructed phylogeny of subgenus *Gaymara* is based on five species (Table 2, Fig. 159). Two characters account for two evolutionary reversals, nine characters account for nine parallelisms.

The ancestral lineage of subgenus *Gaymara* is distinguished by the characters elongate and tridentate labrum with fewer than eight setae, short apical setae on abdominal sternum eight of the female, ventral sclerite of the bursa copulatrix with two elongate posterior projections, both flagellum and small stiffening rib absent from the internal sac of male, membranous tooth of the internal sac, and central plate joined to shield.

The reconstructed phylogeny of the subgenus *Plectographa* (Fig. 160) is based on apomorphous characters of 18 extant South American species listed in Table 2. Two characters account for 34 evolutionary reversals and 16 characters for 91 parallelisms. Broad, fused, ragged and spotted maculations of the elytra, widespread among extant species, appear to have evolved independently at least four times. A large body size, long spermathecal duct, elongate tooth with a spatulate apex and folded laminate shield in the internal sac of the male distinguish the ancestral

lineage of this subgenus. The *eugeni/apiata* lineage stands apart from the others of this subgenus mainly in its primitiveness. The most difficult lineage to place is the monobasic species group *halophila*. Adults of *C. halophila* superficially resemble those of the *suturalis* species group, but male genitalia are radically different. The median lobe is equipped with a short, uncoiled flagellum somewhat similar to that found in North American males of subgenus *Cicindela* and the tooth is short and rounded unlike the type found in *Plectographa* males. A long cuña is present and the shield appears stylet-like. On the other hand female genitalia are similar to those of the *suturalis* species group, particularly in the elongate shape of the ventral sclerite of the bursa copulatrix and presence of approximately eight setae on both apices of sternum 8. Thus the female genitalia were given special weight in selecting an uncertain phylogenetic position for *C. halophila*.

The species *C. siccalacicola*, *C. sinuosa* and *C. suturalis* are probably more closely related than indicated in Figure 160 but we were unable to work out a simpler scheme. On the basis of dense appressed setae on the prosternum and absence of large foveae on the elytra, *C. sinuosa* and *C. suturalis* are established sister species, and, as a consequence, glossy elytra and few erect setae in the middle of abdominal sterna become parallel characters of *C. sinuosa* and *C. siccalacicola*. If weighting of the two former and two latter characters were reversed *C. siccalacicola* and *C. suturalis* would necessarily be treated as sister species.

The species *C. nigrovittata* is tentatively presented as a monobasic species group with ancient links to *Plectographa* lineages. An unusual combination of plesiomorphous and apomorphous characters makes it uniquely different from other species of *Plectographa*. The male genitalia are distinctly *Plectographa*-like in detail. A deep rugosity forming two large swirls or pits on the head between the eyes of the adults indicates an extraordinary convergence with adults of several species in subgenus *Gaymara*.

The reconstructed phylogeny of South American lineages of subgenus *Cylindera* is based on nine species (Fig. 161, Table 2). North American species were not included as a considerable geographical gap exists between them and South American species. We assumed that species in South America are more closely related to each other than to any in North America. The relationships of *C. granulipennis* and *C. malaris* are tentative as their male and female genitalia are not known. An additional 21 and six characters were not determined for these two species and four others respectively. Seven characters account for eight evolutionary reversals and 12 characters for 28 parallelisms.

The ancestral lineage is characterized by elytra slightly glossy with a few foveae, moderately setose proepisternum, average to elongate labrum width, some or all setae of labrum very near front margin, fewer than eight labrum setae, ventral sclerite partly covered with setae and with two anterior lobes and two posterior projections, and shield absent from the bursa copulatrix.

Table 3. Apomorphous characters shared by Brazilian subgenera of *Cicindela**.

Code letter	Subgenera	Characters																										
		3	4	6	7	8	9	14	16	17	19	21	22	27	30	31	32	33	35	36	37	38	41	43	44	45	46	48
A	Brasiella			F^1	G	H	I		P^1 P^2	Q			v^1	a a^1						j^2	k		o	q^1	s	t		v v^1
B	Gaymara	C	D	F	G	H	I	N	P^1	Q	s^1	u^1	v	a	d^1	e	f	g		j^2	k	l	o		s	t		v v^1
C	Plectographa	C	D	F F^1	G	H	I	N	P^1		s^1	u^1		a a^1 a^2 a^3	d^1			g g^1	i				o		r			v v^1
D	Cylindera	C		F F^1				N	P^2	Q		u^1	v	a v^1 a^2 a^3	d^1	e	f	g g^1	i	j^2		l		q^1	r			v v^1

* Characters shared by two subgenera:

AB Brasiella/Gaymara - 37,45,46
AC Brasiella/Plectographa - none
AD Brasiella/Cylindera - 43 (16,22)
BC Gaymara/Plectographa - 4,19
BD Gaymara/Cylindera - 31,32,38 (22)
CD Plectographa/Cylindera - 35,44 (33,27)

Characters shared by three subgenera:

ABC Brasiella/Gaymara/Plectographa - 7,8,9,41 (16,27)
ABD Brasiella/Gaymara/Cylindera - 17,36
ACD Brasiella/Plectographa/Cylindera - none (6,27)
BCD Gaymara/Plectographa/Cylindera - 3,14,21,30,48 (6,33)

NOTE: Brackets indicate gradient characters
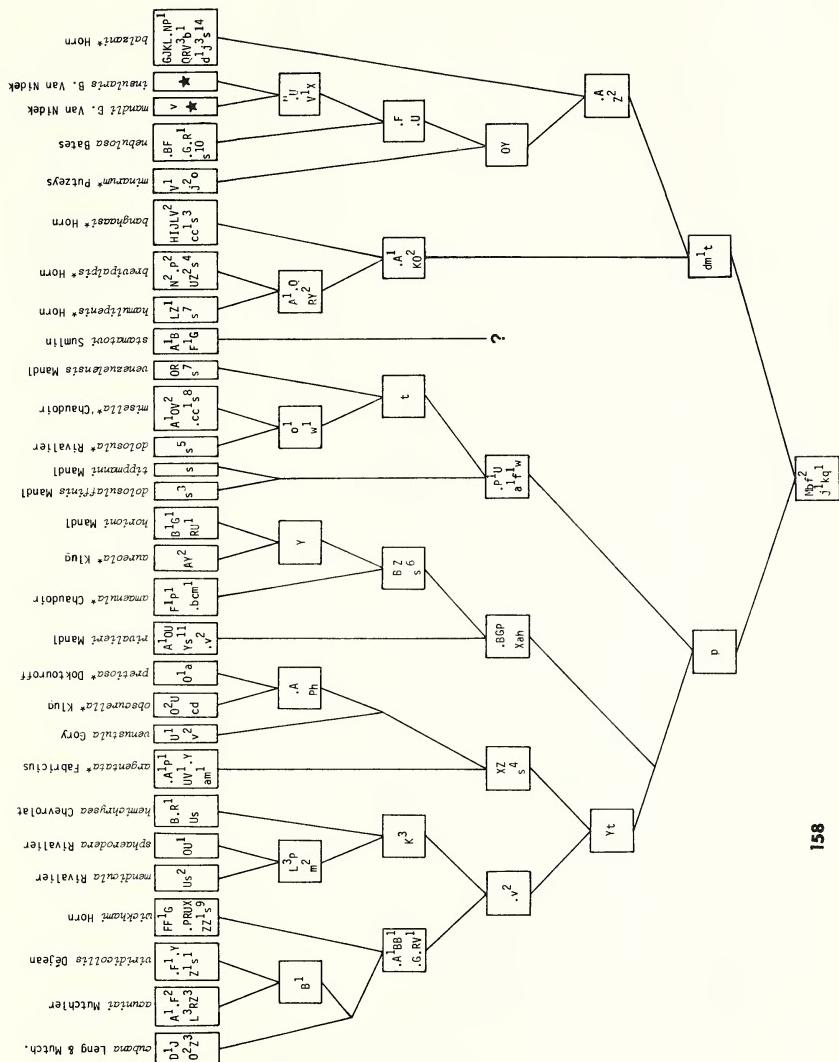
Fig. 158. Phylogenetic diagram for South American species of *Brasiella*. An asterisk indicates Brazilian species. *Cicindela mandli* Brouerius van Nidek has a median lobe with a rounded hook and C. *insularis* Brouerius van Nidek, a median lobe with an abrupt hook (★).

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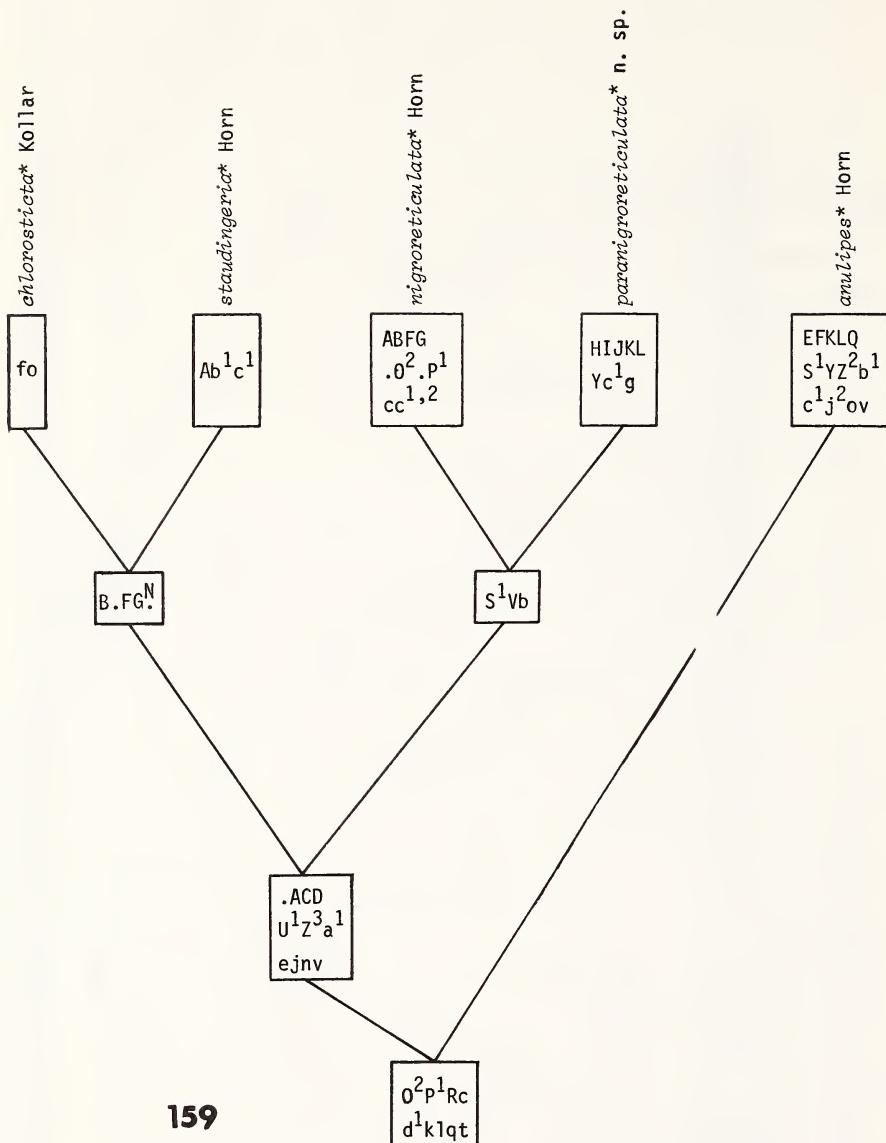
Fig. 159. Phylogenetic diagram for South American species of *Gaymara*. An asterisk indicates Brazilian species.
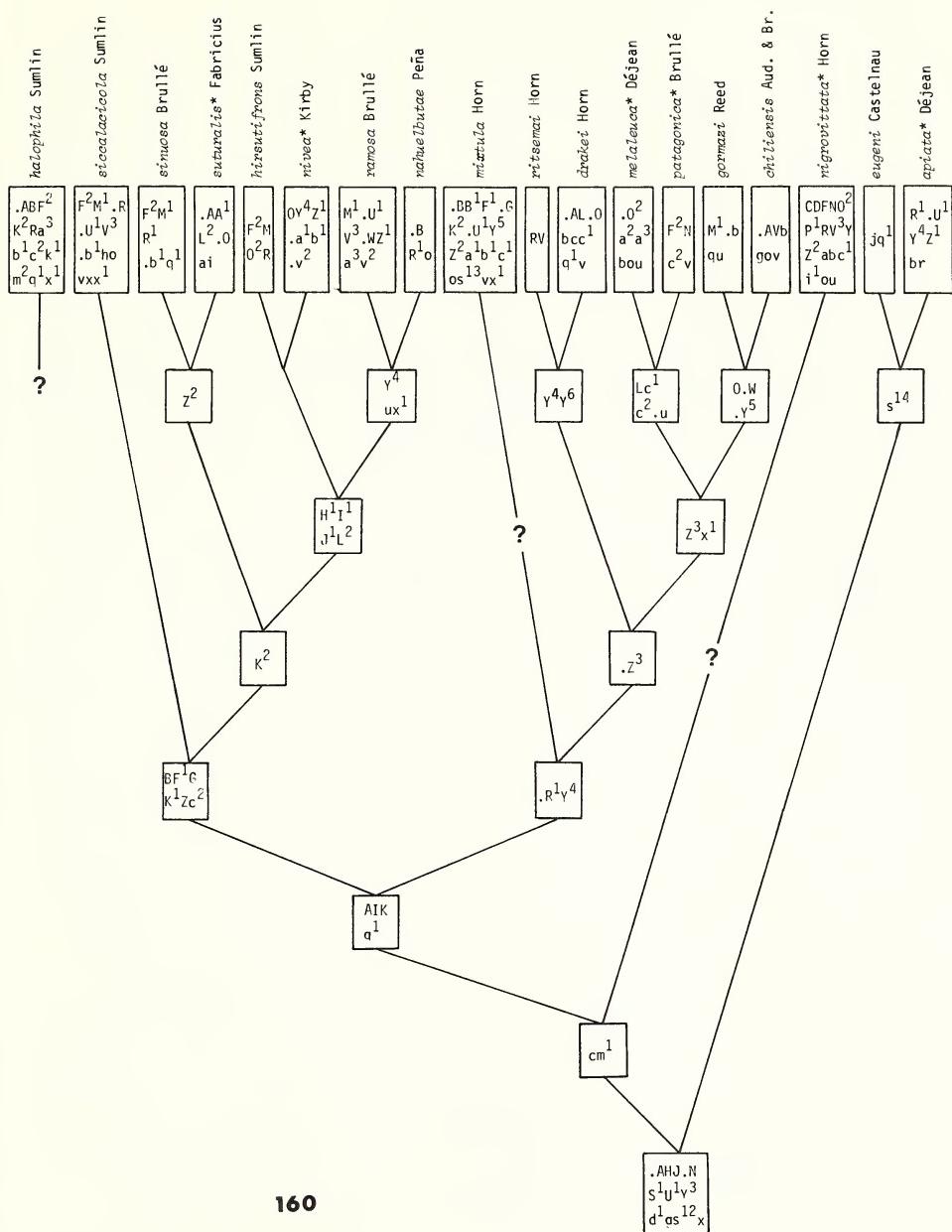
Fig. 160. Phylogenetic diagram for South American species of *Plectographa*. An asterisk indicates Brazilian species.
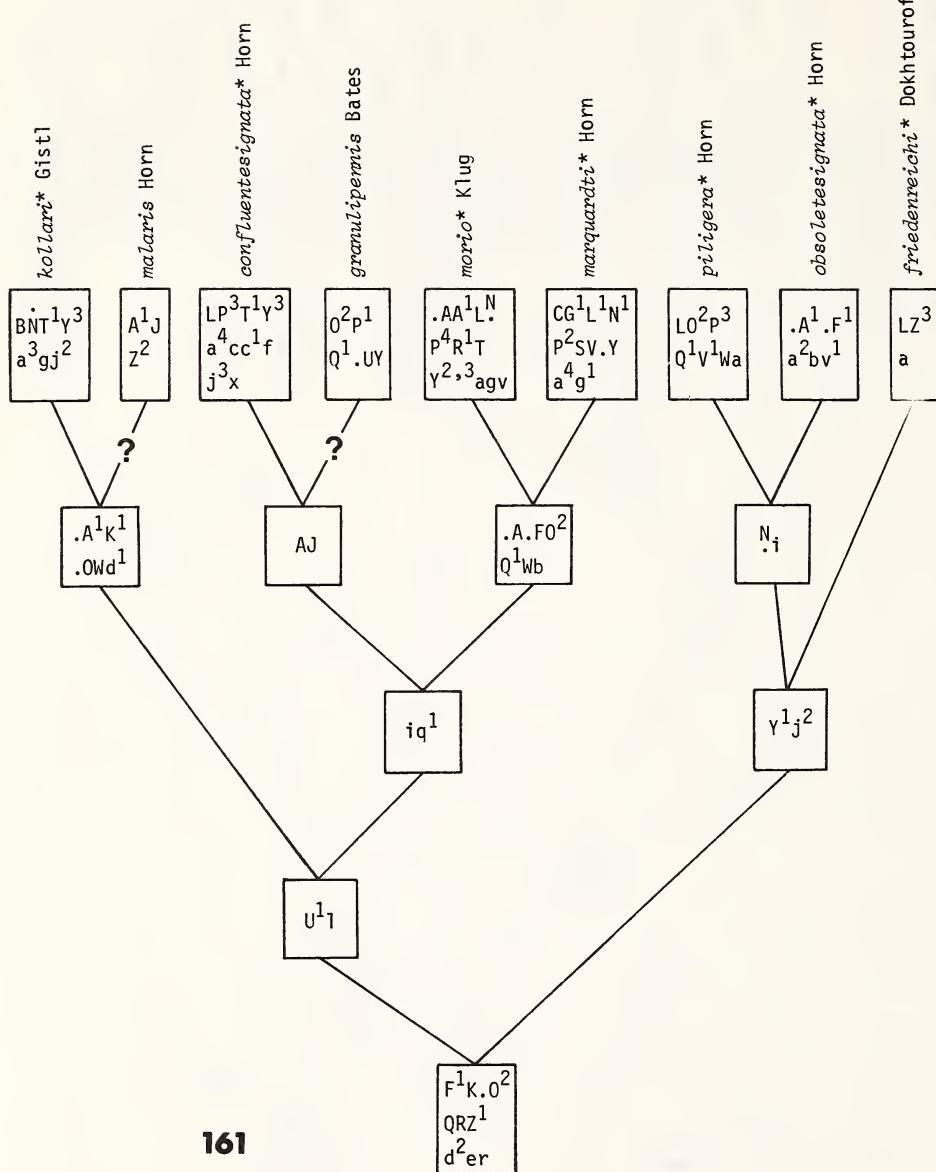
Fig. 161. Phylogenetic diagram for South American species of *Cylindera*. An asterisk indicates Brazilian species.
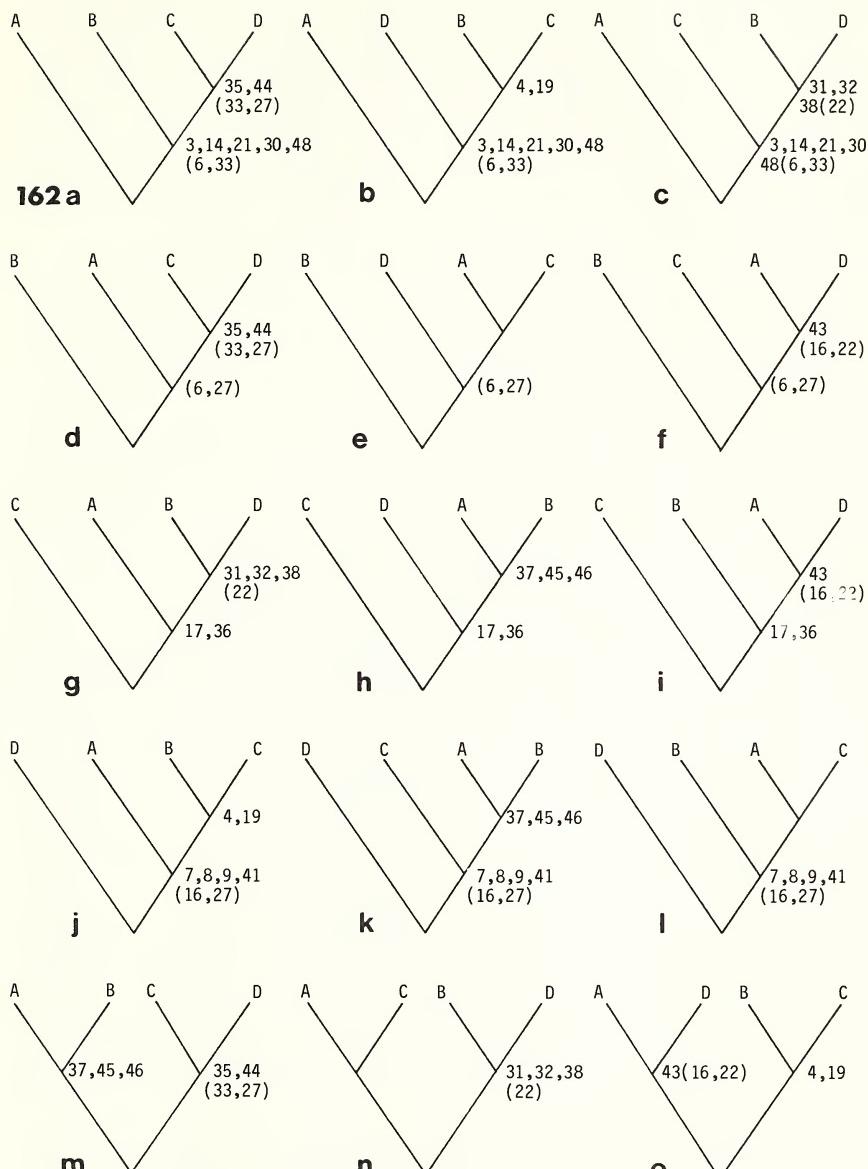
Fig. 162. Fifteen possible dichtomous cladograms for the four subgenera of Brazilian *Cicindela*, and characters in Table 3 for which apomorphous states are shared by members of each subgenus. Letters represent subgenera as follows: A - *Brasiella*, B - *Gaymara*, C - *Plectographa*, D - *Cylindera*. Numbers in brackets indicate gradient characters.
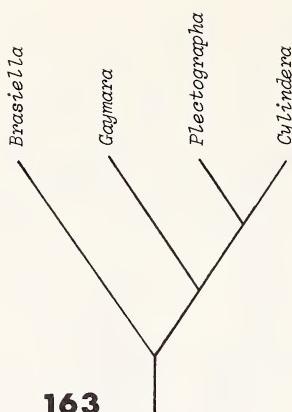
Fig. 163. Phylogenetic tree of the Brazilian subgenera of *Cicindela*.

Inter-group relationships are summarized in Table 3 and Figures 162 and 163. In the construction of Table 3, apomorphous states shared by subgenera, and those which occur in one or more species of a subgenus, were considered as having equal weight. Ideally apomorphous character states indicative of strong relationships are shared by all of most species of related subgenera. These apomorphous character states complement the less frequent apomorphous states. A broad pronotum and ventral sclerite with two elongate posterior projections are shared by most species of *Gaymara*, *Plectographa* and *Cylindera*. The absence of a flagellum and small stiffening rib characterize most species of *Brasiella* and *Gaymara*. All species of *Brasiella* and three of *Cylindera* lack a central plate, and most species of *Gaymara* and *Cylindera* have setae on the ventral sclerite and a membranous tooth.

As shown in Figure 162, of the 15 possible dichotomous cladograms for the four subgenera, either *a* or *c* probably indicates the true phylogeny because they each incorporate the largest number of synapomorphous character states, 11 in each. We favour cladogram *a* as it places the *Gaymara* lineage in an intermediate position between the *Brasiella* lineage and the *Plectographa/Cylindera* lineage, with which the former shares apomorphous character states of the genitalia approximately equally (Figs. 162a, m).

The subgenus *Brasiella* is a Neotropical autochthon that occupies mainly the northern half of South America and Central America where its origins and evolution undoubtedly took place. It is sister of the *Gaymara/Cylindera* lineage (Figs. 162a, 163). *Brasiella* seems to have retained a largely plesiomorphous habitus with several apomorphous acquisitions. The absence of a flagellum in the internal sac of the male is assumed to be an apomorphous state in *Brasiella*. It implies that earlier lineages

had a flagellum which was lost twice, once in *Brasiella* and again in *Gaymara*. If it is assumed that ancestors lacked a flagellum, which was then acquired by the *Plectographa/Cylindera* lineage parallel to and independent of other groups of tiger beetles, it is difficult to account for the complex form of this new flagellum. In more primitive subgenera of *Cicindela* the flagellum is almost straight, but in South American species it has 1.5 loops at the base. Thus we recognize the absence of the flagellum in *Brasiella* as being a loss of a somewhat specialized flagellum. Similarly the membranous oviduct prevalent in *Brasiella* is considered to be a loss of a well developed sclerotized one which is widespread in *Cicindela*.

The subgenus *Gaymara* is endemic to central-eastern South America. It is sister to the *Plectographa/Cylindera* lineage (Figs. 162a, 163). A narrow field-like strip or a membranous "tooth" of the internal sac of the male is present in most species of *Gaymara*, which is remarkably similar to the tooth with a spatulate apex found in species of *Plectographa*. Similarities of this degree are normally given a great deal of taxonomic weight, however, for these taxa it is difficult to conclude that these structures are homologues. If these structures are indeed synapomorphous the true genealogy is probably indicated by Figure 162c rather than Figure 162a.

The subgenus *Plectographa* is sister to subgenus *Cylindera* (Figs. 162a, 163). Most of its species are specialized in a number of characteristics including a broad and ragged pattern of the elytral maculations, and structure of male and female genitalia. This subgenus is endemic to the southern half of South America on both sides of the Andes. *Cicindela suturalis* which ranges from Brazil to the West Indies is the northernmost member of *Plectographa*.

The subgenus *Cylindera* is the only cosmopolitan South American subgenus of *Cicindela*. Most South American species of *Cylindera* live in central-eastern parts of that continent.

The relative age and origins of the subgenera are as follows: *Brasiella*, probable ancient Neotropical endemic, sister group of *Gaymara/Cylindera* lineage, originated in the northern half of South America and Middle America; *Gaymara*, South American endemic, sister group of the *Plectographa/Cylindera* lineage, with Brazilian origins south of the Amazon basin; *Plectographa*, sister group of *Cylindera*, South American endemic, origins in Argentina; *Cylindera*, highly diverse cosmopolitan complex, recent South American lineages probably originated in regions of southeastern Brazil.

BIOGEOGRAPHY

Introduction

Here we offer explanations of geographical distributions of extant taxa, their ancestral origins, and pathways taken to where they now live. This procedure combines current knowledge of geological and climatic history of the Neotropics, geographical distributions of the studied species, and their phylogenetic relationships.

Assumptions

Our integration of these data is based on three assumptions. The first is that origins of South American subgenera of *Cicindela* preceded the Cenozoic Era, no later than early Cretaceous. In addition, early lineages and species groups diversified throughout the Tertiary Period, while extant species evolved during the late Pliocene and Pleistocene, beginning about 2 or 3 million years ago. With the exception of subgeneric origins, these time/lineage associations are in keeping with contemporary ground beetle studies (Ball, 1985; Noonan, 1985; Ball and Shpeley, 1986).

The second assumption is that there has been a general tendency in *Cicindela* for independent lineage adaptations to open country habitats in temperate and tropical regions (Cazier, 1954; Willis, 1967, 1972; Freitag, 1979; and articles in the journal *Cicindela* since 1969). Although riparian and woodland intrusion are plentiful in various groups, they appear to indicate the primitive and intermedia adaptive states respectively. This supports the "taxon cycle" concept demonstrated by carabids as reviewed by Erwin and Adis (1982), in which wetland generalists radiate into a biotic zone away form the waterside substratum and become evolutionary specialists. Specializations in savanna and prairie biomes have been major trends in a broad spectrum of lineages of *Cicindela*. As will be shown, the main distribution patterns of South American lineages of *Cicindela* are closely allied to savanna and open country conditions.

The third assumption is that speciation in *Cicindela* follows the allopatric mode as defined by Mayr (1963), that is geographic speciation. Important to this process are physical or climatic barriers, which isolate conspecific populations from one another, disrupt gene flow among them, and ultimately cause the formation of genetically incompatible separate species.

Hypotheses

Current hypotheses that explain range distributions and geographical histories of South American organisms synthesize past geophysical, climatic, and biotic processes which appear to have had a general influence on their biogeography. (For reviews see Simpson and Haffer, 1978; Webb, 1978; and Haffer, 1981).

One such hypothesis is the Refuge Theory, which postulates that the biotic richness of tropical forests is created by chai 'ng vegetations due to climatic fluxuations (Prance, 1982; Mayr and O'Hara, 86). A special kind of allopatric

speciation is therefore proposed in this theory which discards geophysical factors as part of the diversification process.

There is a growing body of evidence, however, that implies forest disturbance due to modern and past river dynamics is partially responsible for the high biological diversity in the upper Amazon basin (Salo *et al.*, 1986).

As stated by Haffer (1982) the Refuge Theory holds that forest and non-forest biomes changed continuously in distribution during the geological past, breaking up into isolated blocks and again expanding and coalescing under the varying humid to arid climatic conditions of certain geological time intervals, especially during the Quaternary.

Also important is the complex Tertiary geology of Central America. Unresolved are the time of the complete isthmian connection of North and South America and the extent of dry land within the sea gap before the continents were joined. The region appears to have served as island repositories for some evolving groups, and periodic crossings undoubtedly took place throughout the Tertiary, either by island hopping or across wide stretches of ocean. (Howden and Young, 1981, and Ball and Shpeley, 1986, discuss these problems in the light of beetle biogeography and provide references.)

Two hypotheses focus on biogeographic affinities of the Greater Antilles to other parts of the New World. One view, the vicariance model of Caribbean biogeography, is that tectonic forces, during the early or middle Tertiary, displaced portions of the Proto-Greater Antilles (land between North and South America) north-eastward to form the Greater Antilles, and that pieces of the original fauna were taken along as insular inhabitants (Rosen, 1975; Guyer and Savage, 1986).

The older dispersal model of Caribbean biogeography followed here proposes that dispersals from mainland coasts bordering the Caribbean region account for most of the fauna on the Greater Antilles. Records of offshore flights, up to distances of 100 miles by *C. trifasciata* (Erwin, 1979; Graves, 1981) and its wide geographical distribution in the West Indies (Leng and Mutchler, 1916; Elliott and Salbert, 1978); the presence of *C. marginata* in coastal eastern United States, Bahamas, and Cuba (Leng and Mutchler, 1916; Vaurie, 1952); and recent dispersals of *C. carthagena* from Central America or Colombia to Jamaica (Brouerius van Nidek, 1980; Freitag, 1985) and *C. olivacea* from Cuba to Florida (Woodruff and Graves, 1963) are evidence for the dispersal model and examples of the highly volant nature of adult *Cicindela*.

Past Climatic, Floristic and Geophysical Processes

Factors which very likely have had a bearing on the diversification of Neotropical taxa of *Cicindela* are: (1) formation of South America and its westward drift across the Pacific Ocean, following breakup of Gondwanaland in the late Cretaceous (Hallam, 1981); (2) proximal insular connection and eventual joining of North and South America through the Central American land bridge in the late

Table 4. Distribution of species of the subgenus *Brasiella* according to geographic area.* +

Species	N. Argen.	SE. Brazil⊙	Braz. Hghld.	W.Par. E.Bol.	Amazon R.Bas.	N.S. Amer.	NW.S. Amer.	Lo.C. Amer.	Nuc.C. Amer.	Mexico	NW.Mex. SW.U.S.	W.I. Gr.Ant.	W.I. L.Ant.
Area No.	3	4	5	6	7	8	9	10	11	12	13	14	15
viridicollis group													
cubana												V	
acuniai												V	
viridicollis												V	
wickhami											V		
hemichrysea group													
mendicula						V	V	V	V				
sphaerodera								V	V				
hemichrysea								V	V	V			
argentata group													
argentata	V	V	V	V	V	V	V						V
venustula						V							
obscurella	V	V	V										
pretiosa					V								
aureola group													
rivalieri													
amaenula				V	V								
aureola	V	V	V	V	V								
horioni				V									

(continued on next page)

Table 4 (continued)

Species	Area No.	N. Argen.	SE. Brazil Ø	Braz. Hghld ⊙	N.Par. E.Bol.	Amazon R.Bas.	N.S. Amer.	NW.S. Amer.	Lo.C. Amer.	Nuc.C. Amer.	Mexico	NW.Mex. SW.U.S.	W.I. Gr.Ant.	W.I. L.Ant.
Ø Area /		3	4	5	6	7	8	9	10	11	12	13	14	15
misella group														
dolosulaffinis			v											
tippmanni			v											
dolosula		v	v	v	v	v								
misella			v	v	v			v	v					
venezuelensis							v							
stamatovi group														
stamatovi		v												
minarum group														
hamatipenis				v										
brevipalpis				v										
banghaasi				v										
minarum				v										
nebulosa								v	v	v				
mandli										v				
insularis							v							
balzani					v	v								
TOTAL 29		5(1)	6(2)	10(4)	7(1)	6(1)	6(4)	5	6	6(1)	1	1(1)	3(3)	1

* Endemic species are shown in brackets.
\+ References for Tables 4-7: Blackwelder (1944), Fernandez (1936), Mandl (1956, 1963, 1967, 1973), Peña and Barría (1973), Rivalier (1954, 1955), Sumlin (1979), Varas Arangua (1925), Vidal Sarmiento (1966b).
Ø See area description in area section that follows.
⊙ Includes NE. Argentina, E. Paraguay, and Uruguay.

Tertiary; (3) presence of the Guayana and Brazilian shields, which have been above sea level since Paleozoic time (Haffer, 1981); (4) marine ingressions in the Amazon basin from the Atlantic and Pacific Oceans during the early Tertiary (Haffer, 1981); (5) progressive Andean orogeny since the end of the Cretaceous, but principally that of the Pliocene and Quaternary that led to the emergence of lowlands immediately surrounding the Andes (Haffer, 1981); (6) origins of seasonal woodlands and savanna in Patagonia and their gradual spread in South America during the Tertiary and Quaternary (Webb, 1978); and (7) periodic expansions of non-forested areas into the Amazon basin caused by glacial episodes in the Pleistocene (Prance, 1982).

Cenozoic vegetational changes were related directly to cooler and drier climates. The Andean uplift and circulation patterns around 30° S latitude created a rain shadow in temperate South America, and ultimately contributed to the development of desert conditions inland and the driest east coast in the southern hemisphere (Furley and Newey, 1983). Central America and the Amazon basin were not greatly affected by cooling trends in the Tertiary, and a tropical rain forest dominated the land.

Expected Geographical Patterns

Given the above, certain geographical patterns may be expected, as follows: (1) a general fit of vicariance patterns, of any subgenus to the Cretaceous breakup of Gondwana, and of any species group to the coming together of North and South America and to the Guayana and Brazilian shields in the Tertiary; (2) grasslands and open forests to hold the largest number of species as demonstrated by Willis (1972) for North American *Cicindela*; (3) the Amazon basin to be a major region of diversification for Tertiary and Pleistocene lineages; (4) post-Pleistocene refugia or major species centers to be found outside of the Amazon basin.

Distribution and Historical Interpretation – Subgenera

Subgenera *Brasiella*, *Gaymara* and *Plectographa* are Neotropical endemics, and *Cylindera* is Cosmopolitan (Tables 4-7).

Of the first three, *Brasiella* occupies the northern half of South America, Middle America, and the West Indies, *Gaymara* is confined to eastern South America, and *Plectographa* ranges across South America from central Chile and western Patagonia to the West Indies. Subgenus *Cylindera* in South America is confined mainly to Brazil south of the Amazon basin. This subgenus is part of a complex the members of which Rivalier (1950, 1954, 1957, 1961, 1963) treated as subgenera within the genus *Cylindera*. Subgenus *Cylindera s. str.* ranges in both the Old and New Worlds and other members are found in temperate and tropical regions of the Old World (Fig. 164; Table 7).

The reconstructed phylogeny (Fig. 163) shows three dichotomies (divergences): *Brasiella* and lineage *Gaymara - Plectographa - Cylindera*; *Gaymara* and lineage *Plectographa - Cylindera*; and *Plectographa* and *Cylindera*.

The collective distributional pattern of the four subgenera suggests a Gondwanan ancestry. Divergence-spatial relationships among ancestral lineages are obscure as the four subgenera are more or less sympatric in South America. The geographical ranges of *Plectographa* and *Cylindera* might indicate a south-north division of their immediate ancestor in western Gondwanaland.

Concerning the cosmopolitan geography of *Cylindera*, we propose that the break-up of Gondwanaland in the Cretaceous was the initial cause of its disjunctions in the southern hemisphere, that is between South America and Africa, followed by late Cretaceous dispersal from South America into North America, and from Africa into Eurasia during the early and middle Tertiary. (See Hallam, 1981, for a review of plate movement, eustasy, climate, and organic response to them since the early Mesozoic, as background information for the above hypothesis.)

Distribution and Historial Interpretation – Species Groups and Species

Ecological Notes.— Species of *Cicindela* in the Neotropics and elsewhere occupy similar habitats. Ecological requirements are specific and diverse among taxa, though water availablility and soil types are principal factors in governing geographical distributions of species. As a group, members of *Cicindela* are ground residents living in open places in most biomes. Common habitat sites are roadsides, paths in forests, banks of rivers and streams, edges of lakes, ponds, sea beach s and salt marshes, and fields such as grasslands, pastures and salt playas. A few species inhabit mountains, deserts, and low wetlands.

Species of *Cicindela* found in the Amazon River basin are largely ecological generalists. The majority of these species are found in other areas as well. Tiger beetles typical of tropical rain forests such as those of *Odontocheila* and *Ctenostoma*, are arboreal, but species of *Cicindela* are obligate terrestrial forms unsuited to dense forests and long and frequent periods of flooding, characteristic of the Amazon lowlands. Nonetheless the fact that widespread and relict species of *Cicindela* exist in the Amazon River basin indicates a history of establishments there.

Data available for 17 (29%) of 61 species studied indicate spatial patterns of habitat type or habitat factor preference.

Adults of insular and mainland species of the *C. viridicollis* species group (*Brasiella*) are found on patches of bare ground and in dry grasslands. Adults of *C. argentata* are found in moist grassy places and on river beaches.

Adults of sister species *C. melaleuca/C. patagonica (Plectographa)* are found on sea coasts. The former species lives near marshes and dry places inland as well. Three additional species of *Plectographa* are seashore residents and adults of one other have been collected on salt playas. Adults of *C. suturalis* are riparian. The habitats of these species, one third of a total of 18 species, in this subgenus, suggest seaside origins and early development for salt tolerance in *Plectographa*.

Table 5. Distribution of species of the subgenus *Gaymara* according to geographic area.[*]

Species	Area	S.E. Brazil[**]	Braz. Hghld.	Amazon R. Basin
	Area No.	4	5	7
chlorosticta group				
chlorosticta		V	V	V
staudingeria		V	V	V
nigroreticulata		V		
paranigroreticulata		V		
anulipes group				
anulipes		V	V	
TOTAL	5	5(2)	3	2

[*]Endemic species are shown in brackets.
[**]Includes NE. Argentina, E. Paraguay, and Uruguay.

Three species of *Cylindera* are riparian which may be characteristic of the habitats for other species of this subgenus.

The majority of Neotropical taxa of *Cicindela* live in places between sea level and 1500 meters, and a few others live at higher elevations up to 3500 meters.

Taxa of most South American species of *Cicindela* are active in summer in the southern hemisphere, appearing anytime from October to April. Taxa within southern parts of the Amazon River basin are also active in "summer". Taxa north of the basin appear to be active during summer of the northern hemisphere, while those that transcend the basin are active all year emerging in warmer seasons of both hemispheres. We have not overlooked the importance of these findings to investigations of speciation and evolution of *Cicindela* in the tropics. An analysis is beyond the scope of this study however, and for now we refer to the phenomenon as "Hemispheric Control of Phenological Activity in Tropical Regions".

Areas.— Fifteen geographical areas are designated as a basis for analysis of distribution patterns. They are delimited by assemblages of taxa of *Cicindela* or where geographical limits of taxa of *Cicindela* are congruent. Brief accounts of the areas follow (taken from Bates, 1961; Garrett, 1981; and Furley and Newey, 1983). Area numbers are listed with their representative taxa in Tables 4-8.

Table 6. Distribution of species of the subgenus *Plectographa* according to geographic area.*

Species	C. Chile	S. Argen.	N. Argen.	S.E. Brazil**	Braz. Hghld.	W. Par. E. Bol.	Amazon R. Bas.	N.S. Amer.	NW. S. Amer.	W.I. Gr. Ant.	W.I. L. Ant.
Area No.	1	2	3	4	5	6	7	8	9	14	15
halophila group											
halophila			√								
suturalis group											
siccalacicola			√								
sinuosa			√	√							
suturalis				√	√		√	√	√	√	√
hirsutifrons			√		√						
nivea		√	√	√							
ramosa			√	√							
nahuelbutae	√										
melaleuca group											
mixtula			√			√					
ritsemai			√								
drakei			√								
melaleuca			√	√							
patagonica			√	√							
gormazi	√	√									

Table 6 (continued)

Species	C. Chile	S. Argen.	N. Argen.	S.E. Brazil**	Braz. Hghld.	W. Par. E. Bol.	Amazon R. Bas.	N.S. Amer.	NW. S. Amer.	W.I. Gr. Ant.	W.I. L. Ant.
Area No.	1	2	3	4	5	6	7	8	9	14	15
chiliensis	V										
nigrovittata group											
nigrovittata					V						
apiata group											
eugeni			V			V					
apiata			V	V	V	V					
TOTAL	3(1)	3	13(6)	7	4(1)	3	1	1	1	1	1

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*Endemic species are shown in brackets.
**Includes NE. Argentina, E. Paraguay, and Uruguay.

Table 7. Distribution of species of the subgenus *Cylindera* s. str. in South and North America, and *Cylindera* and groups or subgenera elsewhere.*

Species	Area N. Argen.	S.E. Brazil**	Braz. Hghld.	Amazon R. Bas.	Mexico	Nearctic (Can., U.S.A.)	Palearctic	Ethiopian	Oriental	Australia
Area No.	3	4	5	7		6				
morio group										
kollari			v	v						
malaris				v						
confluentesignata		v	v							
granulipennis				v						
morio			v	v						
marquardti			v							
friedenreichi group										
piligera			v	v						
obsoletesignata	v	v								
friedenreichi		v								
other species					5	6	20,3+	13,3+	59,9+	1
TOTAL 9x	1	3(1)	5	5(2)	5	6	20	13	59	1

*Endemic species are shown in brackets.

**Includes NE. Argentina, E. Paraguay, and Uruguay.

+Note second number indicates number of species groups or "subgenera" within or closely related to *Cylindera* s. str. from Rivalier (1950,1954,1957,1961,1963).

xNot including other species.
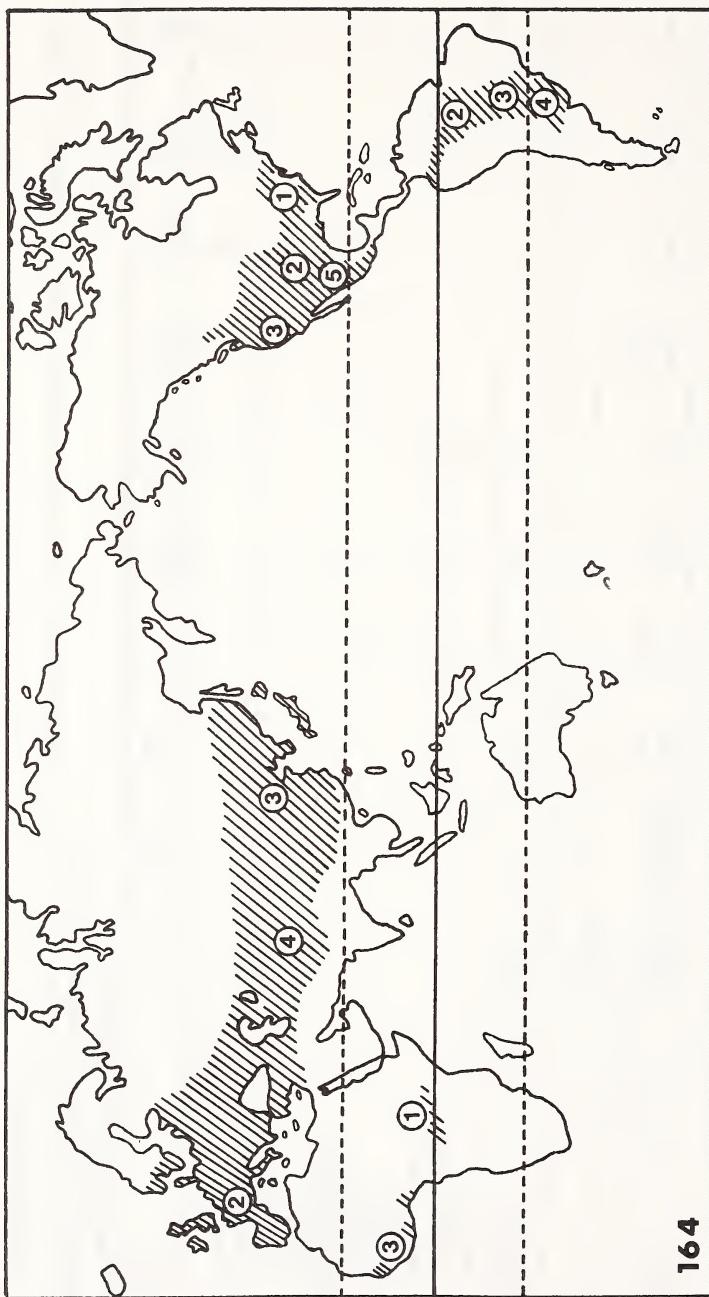
Fig. 164. Distribution of subgenus and species *Cylindera s. str.*

1. Central Chile: Bordered by the west coast and high Andes this is a relatively wet area, south of the Atacama Desert, and consists of coastal forests, eastern upland taiga or tundra, and dry low scrubland in the north. Ball and Shpeley (1986) use the term 'Southern Trans-Andean South America' for this area.

2. Southern Argentina: This area, temperate Patagonia north to approximately Rio Negro, is bordered by the Andes in the west and the east coast. The area is marked by dry western uplands and admixtures of desert, semi-desert and grasslands in central and eastern parts.

3. Northern Argentina: This is the Pampas area. It is bordered by the Andes to the west, the Rio Negro to the south and the east coast. The northern boundary includes Chaco Central and Entre Rios. This is predominantly a grassland region. Semideciduous forests are present in the north.

4. Southern Brazil: This area includes the Brazilian states south of São Paulo, Uruguay, northern Argentina, and eastern Paraguay. The east coast, Entre Rios and Rio Paraguay form the main boundaries. There is no distinct northern boundary. Northern uplands gradually merge with those in the south end of area 5. The vegetational zones are primarily coastal rain forests, prairies to the south, and semideciduous forests to the north.

5. Eastern Brazil (Brazilian Highlands, Brazilian Shield): This vast region to the south of the Amazon River basin, includes the east coast, eastern highlands, and central uplands of Brazil. Western boundaries are Rio Araguaia, the pantanal complex and Rio Paraguay. Semideciduous forests and savanna scrub cover much of this area. Amazonian gallery forests along river valleys extend from the south end of the Amazon basin into northern parts of this area, and extensive rain forests are found on the east coast.

6. Western Paraguay and Eastern Bolivia: This area comprises the Chaco region of both countries and the eastern Bolivian uplands, and is bordered by the Andes to the west, Rio Paraguay to the east, Rio Guaporé to the north, and Chaco central to the south. The region is relatively dry dominated by savanna scrub, and semideciduous forests in central Bolivia, and large river valleys.

7. Amazon River Basin: The area consists of the large upper and main drainage systems of the Amazon River in northern Brazil. A more or less continuous rain forest covers the area. Savanna scrub elements intrude southern and northwestern regions of the basin from areas 5, 6 and 8.

8. Northern South America (Guayana Shield): This area includes the Guayana Highlands, Orinoco River basin, northeastern Colombia, and the north coast of South America. The Andes proper and Cordillera Oriental just west of the Maracaibo basin form the designated western border of this area. Savanna scrub covers western portions. Rain forests and grasslands cover central and eastern parts.

9. Northwestern South America: This area includes Colombia and Ecuador in and west of the Andes. No endemic species of *Cicindela* are found there but geographical ranges of a few species terminate in it. Coastal rain forests and upland

semideciduous forests are widespread, and smaller zones of savanna scrub are present near the Caribbean coast of northern Colombia and Pacific coast of southern Ecuador. Ball and Shpeley (1986) refer to this area as 'Northern Trans-Andean South America'.

10. Lower Central America: This area includes Costa Rica and Panama. A series of islands may have persisted in this area from the mid-Tertiary up until the late Pleistocene. The topography is mixed and consists of central mountains and lowlands. Tropical rain forest is widespread. West of the mountains on the Pacific slope, rainfall and floral richness are reduced.

11. Nuclear Central America: Most of this area, between the Isthmus of Tehuantepec and southern Nicaragua, has been dry land throughout the Tertiary (Rosen, 1978), but periodically separated from Mexico (area 12) by high sea levels (Ball and Shpeley, 1986).

12. Mexico north of the Isthmus of Tehuantepec.

13. Northwestern Mexico and Southwestern United States.

14. West Indies: Greater Antilles.

15. West Indies: Lesser Antilles.

Undesignated areas which are devoid of species are the dry west coast from southern Ecuador to northern Chile, high Andes, and the southern end of Argentina and Chile.

The Distributional Pattern.— Five of the seven *Brasiella* species groups designated, reside chiefly within the northern half of South America (Table 4). Of these, species groups *aureola* and *stamatovi* are endemic to the continent (areas 3-8, and 3 respectively), species groups *minarum* and *misella*, extend into Middle America (areas 3-11), and species group *argentata* is also found in southern islands of the Lesser Antilles (areas 3-9, 15). Of the two remaining *Brasiella* species groups, *hemichrysea* group is primarily Middle American (areas 9-12), and *viridicollis* group is broadly disjunct being present both in Cuba (area 14), and northwestern Mexico and southwestern United States (areas 12, 13). Thus in terms of *Brasiella* species groups the greates iversity is in the northern half of South America.

The 29 species of *Brasiella* collecti y range from northern Argentina to southwestern United States and the West Indies (Table 4). Of the 22 species known from South America, 12 are found south of the Amazon River basin (areas 3-6), four are within or on the edge of the basin (area 7), and six inhabit northern and northwestern South America (areas 8-9). Among the remaining seven species, three are confined to Central America and southern Mexico (areas 10-12), one inhabits northwestern México and southwestern United States (area 13), and three species are found in Cuba (area 14).

The pattern of diversity comprises chiefly two species aggregates in South America. One, south of the Amazon River basin (areas 4-6) diminishes in species number abruptly southward and gradually northward and eastward. A smaller

species aggregate north of the basin is confined largely by the Guayana Highlands and the Andes (area 8).

In closer scrutiny, of the 12 species south of the Amazon River basin four have substantial geographical ranges. The species *C. amaenula* and *aureola* are each widely disjunct with isolated populations in the basin (Fig. 49), *C. obscurella* ranges into southern Uruguay and northern Argentina (Fig. 48), and *C. minarum* is found from near the coast to the Vacaria River area in Matto Grosso (Fig. 51). The remaining eight species have restricted or disjunct ranges. They are *C. horioni* (Bolivia), *C. balzani* (Bolivia, Ecuador), both on the margins of the Amazon basin, *C. dolosulaffinis* and *C. tippmanni* (Paraguay), *C. stamatovi* (northwestern Argentina), and *C. banghaasi*, *C. brevipalpis* and *C. hamulipenis* (southeastern Brazil) (Fig. 51). The species *C. dolosula* and *C. misella* are found south, north and northwest of the Amazon basin and occur in parts of Central America (Fig. 50).

The Amazon River basin is occupied by one widespread species and one local species. The species *C. argentata* is the only species of *Cicindela* found in the arid northeastern parts of area 5, and it extends into the Caribbean region (Fig. 47). The species *C. pretiosa* is found only in the Manaus area (Fig. 48).

Among the six species that inhabit the region north and northwest of the Amazon River basin those with comparatively larger geographical ranges, *C. mendicula* (Nicaragua to western Venezuela) and *C. nebulosa* (Nicaragua to Colomb i and Ecuador), are found in Central America and *C. venustula* occupies the region north of the Guayana Highlands. The species *C. rivalieri* and *C. venezuelensis* are confined to small areas in Venezuela, and *C. insularis* is found in Trinidad and on the adjacent mainland.

Two species have local distributions in Central America and southern México, *C. sphaerodera* in the Quiché Mountains of Guatemala and *C. mandli* in Chiapas, México. *C. hemichrysea* ranges more widely from western México to Panamá. In the north *C. wickhami* inhabits northwestern México and southwestern United States, and *C. acuniai*, *C. cubana* and *C. viridicollis* occupy Cuba.

Nine species are endemic in the southern end of the *Brasiella* range, eight may be geographical relicts (Table 4). Four endemic species are found north of the Amazon River basin. Three of them are probably geographical relicts. At the northern end of the range there is one mainland endemic species, and three species, very likely autochthonous, on Cuba. Only one endemic species is present in Central America.

These findings indicate that the region south and southeast of the Amazon River basin (areas 4-6) has been the chief center of diversification for *Brasiella*. A smaller region north of the basin (area 8) has been a minor center.

The only two species groups of subgenus *Gaymara*, *chlorosticta* and *anulipes*, are found in eastern South America. The species have a composite range mainly in Brazil south of the Amazon River basin (areas 4-5) (Table 5). The area of greatest diversity is Rio Grande do Sul (area 4) in which at least three and probably all five

species exist (Fig. 77). Three species, *C. chlorosticta*, *C. staudingeria* and *C. anulipes*, are comparatively widespread and enter the southern margins of the Amazon River basin (area 7). Two species, *C. nigroreticulata* and *C. paranigroreticulata*, appear to have local ranges.

It is concluded from these data that the major center of diversity for *Gaymara* has been southeastern Brazil (area 4).

Of subgenus *Plectographa*, species groups *suturalis*, *melaleuca* and *apiata*, range largely within northern Argentina (area 3). Species group *halophila* is endemic there, and species group *nigrovittata*, is endemic to southeastern Brazil (area 5). Species group diversity in *Plectographa* is therefore greatest in northern Argentina (Table 6).

The composite geographical range for the 18 *Plectographa* species covers most of South America from temperate Chile and Patagonia to the north coast and West Indies (Table 6). Thirteen species are resident in northern Argentina (area 3); three species are known from Chile (area 1); one species is found in eastern Brazil (area 5); and one species is widespread in the northern half of South America and the West Indies (areas 4-8, 15).

The pattern of diversity consists principally of a large species aggregate in northern Argentina. Species decline in number from this region, abruptly northward and southward, but more gradually eastward.

Of the 13 species in northern Argentina three, *C. drakei*, *C. ritesmai* and *C. mixtula* are found in the west end of this region and the latter species also inhabits Bolivia and possibly western Paraguay. Three species *C. siccalacicola*, *C. hirsutifrons* and *C. eugeni* appear to have restricted ranges, mainly in Cordoba. Intrusions into the eastern portions of northern Argentina, or Paraguay, Uruguay, and southeastern Brazil have been made by *C. halophila*, *C. sinuosa, C. ramosa, C. melaleuca* (Fig. 113), and *C. apiata* (Fig. 114). The species *C. patagonica* seems to be confined to Rio Grande do Sul, Buenos Aires and southern Uruguay (Fig. 113). The coastal species *C. nivea* ranges from Patagonia to Brazil (Fig. 112).

Of the three Chilean species, *C. nahuelbutae* is found locally in Arauco Province, and *C. chiliensis*, and *C. gormazi* extend into southwestern Argentina.

The species *C. nigrovittata* inhabits a small area in eastern Brazil (Fig. 114), and *C. suturalis* is widespread north of Argentina (Fig. 112).

These data show that all or part of the geographical ranges of 13 species are located in the northern half of Argentina (area 3), and two others in southwestern Argentina (area 2). Only three species live entirely outside of northern Argentina. In terms of endemism, six species are located in northern Argentina (area 3), in which three are geographical relicts. One species is endemic to Chile (area 1) and another to eastern Brazil (area 5), both are geographical relicts.

This leads us to conclude that northern Argentina has been the major center of diversity for *Plectographa*.

South American species groups of subgenus *Cylindera*, *morio* and *friedenreichi*, are endemic to the northern half of South America, and occupy mainly southeastern and eastern Brazil (areas 4, 5), Amazon basin (area 7), and marginally, northern Argentina (area 3).

As a group the nine species of South American *Cylindera* range across the middle area of the continent south of the Amazon River from southeastern Brazil to Ecuador and Peru (Table 7). Six species are found in southeastern Brazil (areas 4, 5). One species is found both in southeastern Brazil and Ecuador (areas 5, 7). One species is found in Ecuador (area 7), and one other in Peru (area 7).

The pattern of species diversity consists of a broad aggregate in southeastern Brazil and three isolated taxa in western South America.

Of the seven species found in southeastern Brazil, *C. kollari* and *C. morio* enter southern parts of the Amazon River basin (Figs. 155, 156), *C. confluentesignata* ranges near the coast into Uruguay (Fig. 155), *C. marquardti* is found in Matto Grosso (Fig. 156), *C. friedenreichi* exists as a small isolated population at the south end of this region in Rio Grande do Sul (Fig. 157), *C. piligera* is widely disjunct, found only in Minas Gerais and Ecuador (Fig. 157), and *C. obsoletesignata* ranges into southern Paraguay and northern Argentina (Fig. 157).

The non-Brazilian species *C. granulipennis* and *C. malaris* found in Ecuador and Peru respectively, along with the Ecuadoran *C. piligera* population, represent western area 7 (Amazon basin) isolates of South American *Cylindera*. None of these three taxa appears to exist west of the Andes.

Based on these data we conclude that the major center of diversity for taxa of South American *Cylindera* has been southeastern Brazil (areas 4, 5).

Geographical distributions of species per designated area and endemism of species for the four subgenera collectively indicate a consistent pattern (Table 8, Fig. 165). Northern Argentina (area 3), southeastern Brazil (area 4) and eastern Brazil (area 5) are the major centers of taxa concentration. They contain the largest number of species, about 20 in each area.

Together these areas also contain the largest number of endemic species determined, 17 (54%) of a maximum number of 31 found in all designated areas. Endemism based on species found only in each area is remarkably high, 37% for area 3, 24% for area 4, and 23% for area 5. Fourteen species are found in the Amazon River basin (area 7), and three species (21%) are endemic. Next in importance is northern South America (area 8), in which four (57%) of seven species are endemic. Northwestern South America (area 9) and lower Central America (area 10), each containing six species, are noted for their lack of endemic species. Nuclear Central America (area 11) contains six species including one endemic (17%). Three species are endemic to Cuba, (area 14). One endemic species (10%) of 10 is found in area 6. Other areas (1,2,12,13,15) with three or fewer species have one or no endemic species.

Table 8. Number of species and endemic species of subgenera *Brasiella*, *Gaymara*, *Plectographa*, and *Cylindera* for designated geographical areas.

Taxa	Geographical Area															Total
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
Species	3	3	19	21	22	10	14	7	6	6	6	1	1	4	2	–
Endemic Species	1	–	7	5	5	1	3	4	–	–	1	–	1	3	–	31

Phylogenetic - Geographical Relationships and Areas of Diversification

Allopatric patterns of sister lineages, derived in the phylogenetic section, are important to the identification of geographical origins and regions of diversification. Figure 166 and Tables 9-12 show comparative geographical positions for sister lineages of the studied subgenera. Geographical areas 1 to 15 · e the basis for allopatric reference. Allopatric states of sister taxa between and ʋithin the same geographical area are included.

Beginning with subgenus *Brasiella* (Table 9), two pairs of early sister lineages have allopatric members. One pair is divided between areas 7 and 9 with a small overlap in area 8. Another pair is allopatric in area 12.

Within species groups there are allopatric members in 13 sister lineages. Based on nearest areas of these disjunct sister lineages, the area combinations are, three 7/8, two 5/5, two 11/11, and one each of 5/7, 5/9, 6/7, 5/6 or 7/9, 8/11, and 13/14.

Concerning individual areas alone, nine are associated with allopatric sister lineages in *Brasiella*. The areas with their respective number of allopatric associations shown in brackets are as follows: area 7 (7), area 5(5), area 8(4), area 11(3), a. ea 9(3), area 6(2), area 12(1), area 13(1), and area 14(1).

For *Brasiella* lineages then, the main areas in and among which diversification has occurred are the Amazon River basin (area 7), eastern Brazil (area 5), northern Brazil (area 8), and the junction of Central and South America (area 9 to 11) (Fig. 116).

With the exception of *C. nigroreticulata*/*C. paranigroreticulata*, all members of sister lineages in *Gaymara* are sympatric in areas 4, 5 or 7 (Table 10). The former sister species are allopatric in central parts of southwestern Brazil (area 4) which probably has been the principal area of diversification for the subgenus as the other three species of *Gaymara* exist there as well.

Members of three pairs of *Plectographa* sister lineages are allopatric (Table 11). Their nearest area combinations are 3/1, 3/1 or 2, and 3/4. Area 3 is associated with all three allopatric combinations, and sympatric sister lineages are most frequently found there. Thus we conclude that diversification of the majority of *Plectographa* lineages has taken place in or adjacent to northern Argentina (area 3).

Four pairs of *Cylindera* sister species have allopatric members (Table 12), for which nearest area combinations are 3 or 4/5, 7, 4/4, 4 or 5/7, and 7/7. Based on these data diversification of *Cylindera* lineages has been prominent in or among the Amazon River basin (area 7), southwestern Brazil (area 4), and eastern Brazil (area 5).

As expected, among the principal centers of species diversification the Amazon basin appears to have played a major role, particularly during the Pleistocene. Additional evidence of late Pleistocene effects are the small refugia on the eastern slopes of the Andes along the edges of the Amazon basin, in Bolivia, Peru, and Ecuador. A few species appear to be wedged between the high mountain and rainforest barriers (*i.e., C. balzani, C. granulipennis, C. horioni, C. malaris,* and western populations of *C. piligera*).

There is at least one small refugium within the basin near Manaus, that of *C. pretiosa*, and isolated populations of *C. amaenula* and *C. aureola*.

Sister groups residing on opposite sides of the Amazon basin are evidence of Amazonian disruptions of widespread ancestral lineages, as for example *C. minaum/nebulosa-mandli-insularis*.

Geographical History

Historical aspects of geography for taxa of the four subgenera are pieced together from the above reconstructed phylogeny, assumptions, hypotheses, evidence for past climates and geophysical processes of the Neotropics, and distribution patterns of related and unrelated taxa.

We propose the following events for *Brasiella*. (1) Early Tertiary vicariances of early lineages caused by marine ingressions in the Amazon basin, and founder dispersals over tropical forests in developing open forest and savanna, resulting in diversification of ancestral stocks into *cubana-pretiosa* lineage, *aureola* group, *misella* group, *stamatovi* group, and *minarum* group. (2) Early Tertiary vicariance of *cubana-pretiosa* lineage and its diversification into ancestors of northern South American (Guayana Shield, area 8) *cubana-hemichrysea* lineage and eastern Brazil (Brazilian Shield, area 5) *argentata* group. (3) Diversification of *cubana-hemichrysea* lineage in northern South America, and a middle Tertiary ocean crossing to Central America resulting in North American *viridicollis* group and South American stock of *hemichrysea* group. (4) Dispersal into northern México and diversification of *viridicollis* group, a late Tertiary ocean crossing to Cuba from eastern México or the United States by *cubana-viridicollis* lineage and its Pleistocene diversification on Cuba, and extinctions of southern and eastern

Table 9. Phylogenetic – distributional relationships of *Brasiella* sister lineages.

Sister Lineages	Geographical Areas	Distributional Relationships of Lineages
Species Groups		
C. viridicollis group		
C. acuniai/C. viridicollis	14	sympatric
C. cubana/acuniai-viridicollis	14	sympatric
C. wickhami/cubana-acuniai-viridicollis	12-13/14	allopatric
C. hemichrysea group		
C. mendicula/C. sphaerodera	8-9-11/11	allopatric
C. hemichrysea/mendicula-sphaerodera	10-11-12/8-9-11	sympatric
C. argentata group		
C. obscurella/C. pretiosa	4-5/7	allopatric
C. venustula/obscurella-pretiosa	8/4-5-7	allopatric
C. argentata/venustula-obscurella-pretiosa	3 to 8/4-5-7-8	sympatric
C. aureola group		
C. aureola/C. horioni	3-4-5-7/6	allopatric
C. amaenula/aureola-horioni	5-6-7/3 to 7	sympatric
C. rivalieri/amaenula-aureola-horioni	8/3 to 7	allopatric
C. misella group		
C. dolosulaffinis/C. tippmanni	4/4	sympatric
C. dolosula/C. misella	3 to 7-9-10/6-7-9-10-11	sympatric
C. venezuelensis/dolosula-misella	8/3 to 7-9-10-11	allopatric
dolosulaffinis-tippmanni/venezuelensis-dolosula-misella	4/3 to 10	sympatric

Table 9 (continued)

Sister Lineages	Geographical Areas	Distributional Relationships of Lineages
C. stamatovi group		
C. stamatovi	3	
C. minarum group		
C. hamulipenis/*C. brevipalpus*	5/5	allopatric
C. banghaasi/*hamulipenis-brevipalpus*	5/5-5	allopatric
C. mandli/*C. insularis*	11/8	allopatric
C. nebulosa/*mandli-insularis*	9-10-11/8-11	allopatric
C. minarum/*nebulosa-mandli-insularis*	5/8 to 11	allopatric
C. balzani/*minarum-nebulosa-mandli-insularis*	6-7/5-8 to 11	allopatric
hamulipenis-brevipalpus-banghaasi/ *balzani-minarum-nebulosa-mandli-insularis*	5/5-11	sympatric
Early Lineages		
cubana-wickhami/*mandicula-hemichrysea*	12-13-14/8 to 12	allopatric excl. 12
cubana-hemichrysea/*argentata-pretiosa*	8 to 14/3 to 8	allopatric excl. 8
cubana-pretiosa/*rivalieri-horioni*	3 to 14/3 to 8	sympatric
cubana-horioni/*dolosulaffinis-venezuelensis*	3 to 14/3 to 10	sympatric
cubana-venezuelensis/*hamulipenis-balzani*	3 to 14/5 to 11	sympatric

Table 10. Phylogenetic - distributional relationships of *Gaymara* sister lineages.

Sister Lineages	Geographical Areas	Distributional Relationships of Lineages
Species Groups		
C. chlorosticta group		
C. chlorosticta/C. staudingeria	4–5–7/4–5–7	sympatric
C. nigroreticulata/	4/4	allopatric
C. paranigroreticulata		
chlorosticta-staudingeria/	4–5–7/4	sympatric
nigroreticulata-paranigroreticulata		
C. anulipes group		
C. anulipes	4–5	
Early Lineages		
chlorosticta-paranigroreticulata/	4–5–7/4–5	sympatric
C. anulipes		

mainland populations of *viridicollis* group. (5) Post middle Tertiary dispersal of *hemichrysea* group stock across ocean into Central America and its diversification there, extinctions of elements on the South American mainland, and a Pleistocene reinvasion of *mendicula-sphaerodera* lineage into western Colombia. (6) Vicariance, dispersal and diversification from middle Tertiary through the Pleistocene by the *argentata* group, *aureola* group, *misella* group, and *minarum* group, within and among the three main centers of taxa concentration, northern South America (area 8, Guayana Shield), eastern Brazil (area 5, Brazilian Shield), and the Amazon basin (area 7), mainly relation to expanding open forests and savanna and their intermittent intrusio into the Neotropical rainforests. (7) Pliocene vicariance of ancestral lineage of c nebulosa/mandli-insularis by Andean orogeny in northwestern South America resulting in *C. nebulosa* west of the Andes and ancestor of *mandli-insularis* east of the Andes, and a Pleistocene founder dispersal by the latter across the Andes into middle America resulting in *C. mandli* and *C. insularis.*

Extensive sympatry among sister lineages obscures the geographical history of *Gaymara*. It is likely that southeastern Brazil was the region in which its diversification took place, given that all extant taxa exist there.

Distribution patterns of the taxa and phylogenetic-distributional relationships imply a general history for *Plectographa* in northern Argentina. Late Tertiary dispersals   westward   across   the   Andes   by   the   ancestral   stocks   of

Table 11. Phylogenetic - distributional relationships of *Plectographa* sister lineages.

Sister Lineages	Geographical Areas	Distributional Relationships of Lineages
Species Groups		
C. halophila group		
C. halophila	3	
C. suturalis group		
C. sinuosa/C. suturalis	3–4/3 to 9–14–15	parapatric
C. hirsutifrons/C. nivea	3/2 to 5	allopatric
C. ramosa/C. nahuelbutae	3–4/1	allopatric
hirsutifrons-nivea/ramosa-nahuelbutae	2 to 5/1–3–4	sympatric
sinuosa-suturalis/hirsutifrons-nahuelbutae	3 to 9–14–15/1 to 5	sympatric
C. siccalacicola/sinuosa-nahuelbutae	3/1 to 9–14–15	sympatric
C. melaleuca group		
C. ritsemai/C. drakei	3/3	sympatric
C. melaleuca/C. patagonica	3–4/3–4	sympatric
C. gormazi/C. chiliensis	1–2/1–2	sympatric
melaleuca-patagonica/gormazi-chiliensis	3–4/1–2	allopatric
ritsemai-drakei/melaleuca-patagonica-gormazi-chiliensis	3/1 to 4	sympatric
C. mixtula/ritsemai-chiliensis	3/1 to 4	sympatric

Table 11 (continued)

Sister Lineages	Geographical Areas	Distributional Relationships of Lineages
C. nigrovittata group		
C. nigrovittata	5	
C. apiata group		
C. eugeni/C. apiata	3/3 to 6	sympatric
Early Lineages		
siccalacicola-nahuelbutae/mixtula-chiliensis	3 to 9–14–15/1 to 4	sympatric
siccalacicola-chiliensis/nigrovittata	1 to 9–14–15/5	sympatric
siccalacicola-nigrovittata/eugeni-apiata	1 to 9–14–15/3 to 6	sympatric

Table 12. Phylogenetic - distributional relationships of *Cylindera* sister lineages.

Sister Lineages	Geographical Areas	Distributional Relationships and Lineages
Species Groups		
C. morio group		
C. kollari/C. malaris	5–7/7	allopatric
C. confluentesignata/		
C. granulipennis	4–5/7	allopatric
C. morio/C. marquardti	5–7/5	sympatric
confluentesignata-granulipennis/		
morio-marquardti	4–5–7/5–7	sympatric ?
kollari-malaris/		
confluentesignata-marquardti	5–7/4–5–7	sympatric
C. friedenreichi group		
C. piligera/C. obsoletesignata	5–7/3–4	allopatric
C. friedenreichi/		
piligera-obsoletesignata	4/3–4–5–7	allopatric
Early Lineages		
kollari-marquardti/		
piligera-friedenreichi	4–5–7/3–4–5–7	sympatric

melaleuca-patagonica/gormazi-chiliensis and of *C. ramosa/C. nahuelbutae* resulted in the Chilean species *C. gormazi*, and the stock of *C. chiliensis/C. nahuelbutae* which diversified west of the Andes, and resulted in the latter sister species.

Sympatric relationships of sister lineages of relative early and intermediate age obscure historical events of *Cylindera*. Allopatric relationships of recent lineages however indicate the following events: (1) Pleistocene vicariance and diversification of stock of *C. kollari/C. malaris* caused by expansions of rainforest during an interglacial phase resulting in Amazon basin species *C. kollari* (east) and *C. malaris* (west). (2) Events as in (1) for stock of *C. confluentesignata/C. granulipennis* resulting in *C. confluentesignata* (east Brazil) and *C. granulipennis* (Ecuador). (3) Vicariance and diversification of ancestral stock of *C. friedenreichi/C. piligera-C. obsoletesignata* in southeastern Brazil during Pliocene or early Pleistocene, possibly as a result of habitat decrease caused by increased aridity in eastern Brazil, resulting in *C. friedenreichi* and stock of *C. piligera/C. obsoletesignata*, and vicariance of the latter resulting in *C. piligera* and *C. obsoletesignata*. (4) Dispersal of *C. piligera*
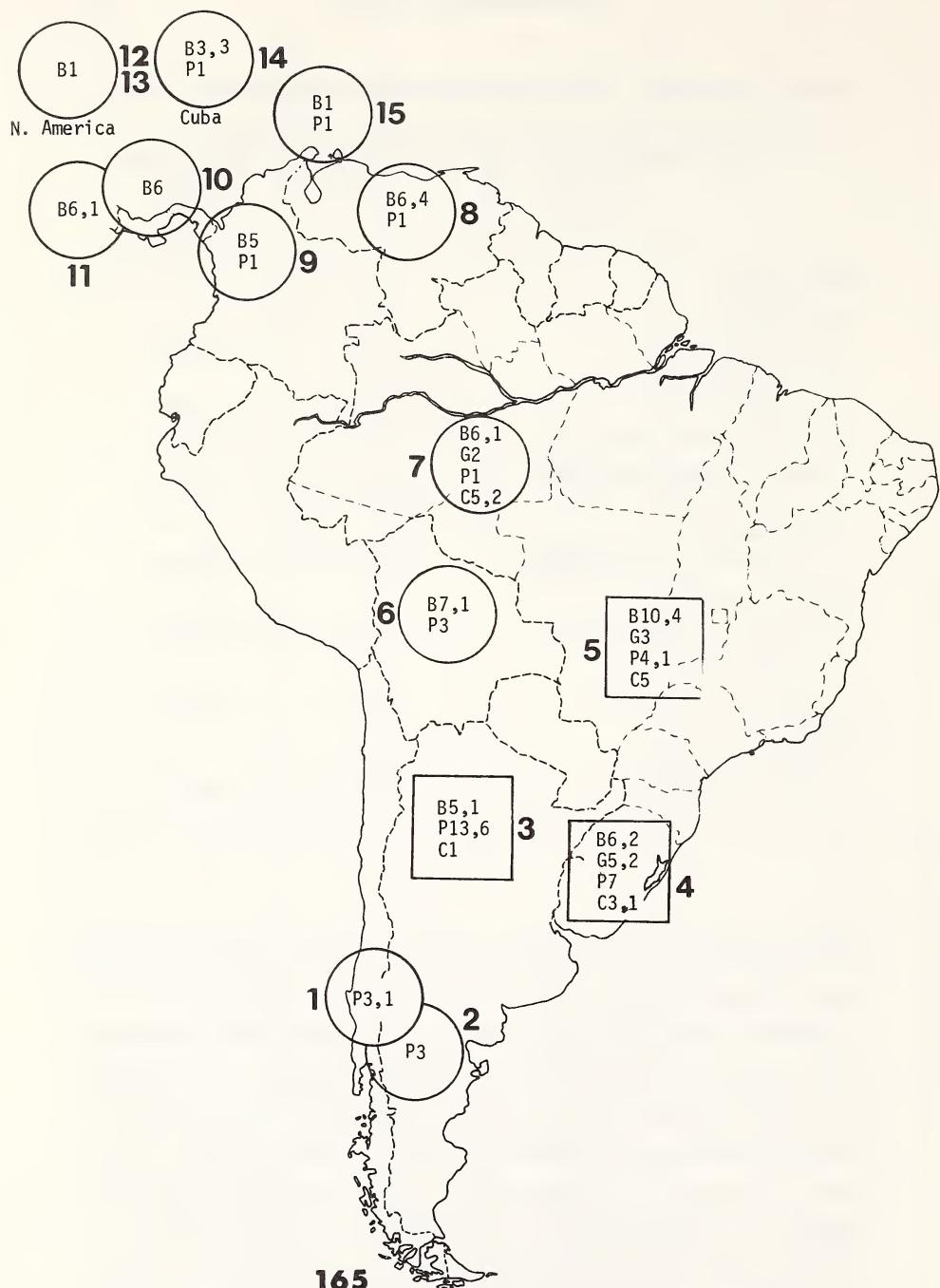
Fig. 165. Distribution of species of *Brasiella*, *Gaymar⟨   lectographa*, and *Cylindera* according to geographical area. Symbols: the number beside a circle d⟨   ⟩s geographical area; squares and circles are major and minor centres of species concentration respec⟨   ⟩ly; letters denote subgenus; first and second numbers beside letters denote number of species and endemic species respectively.
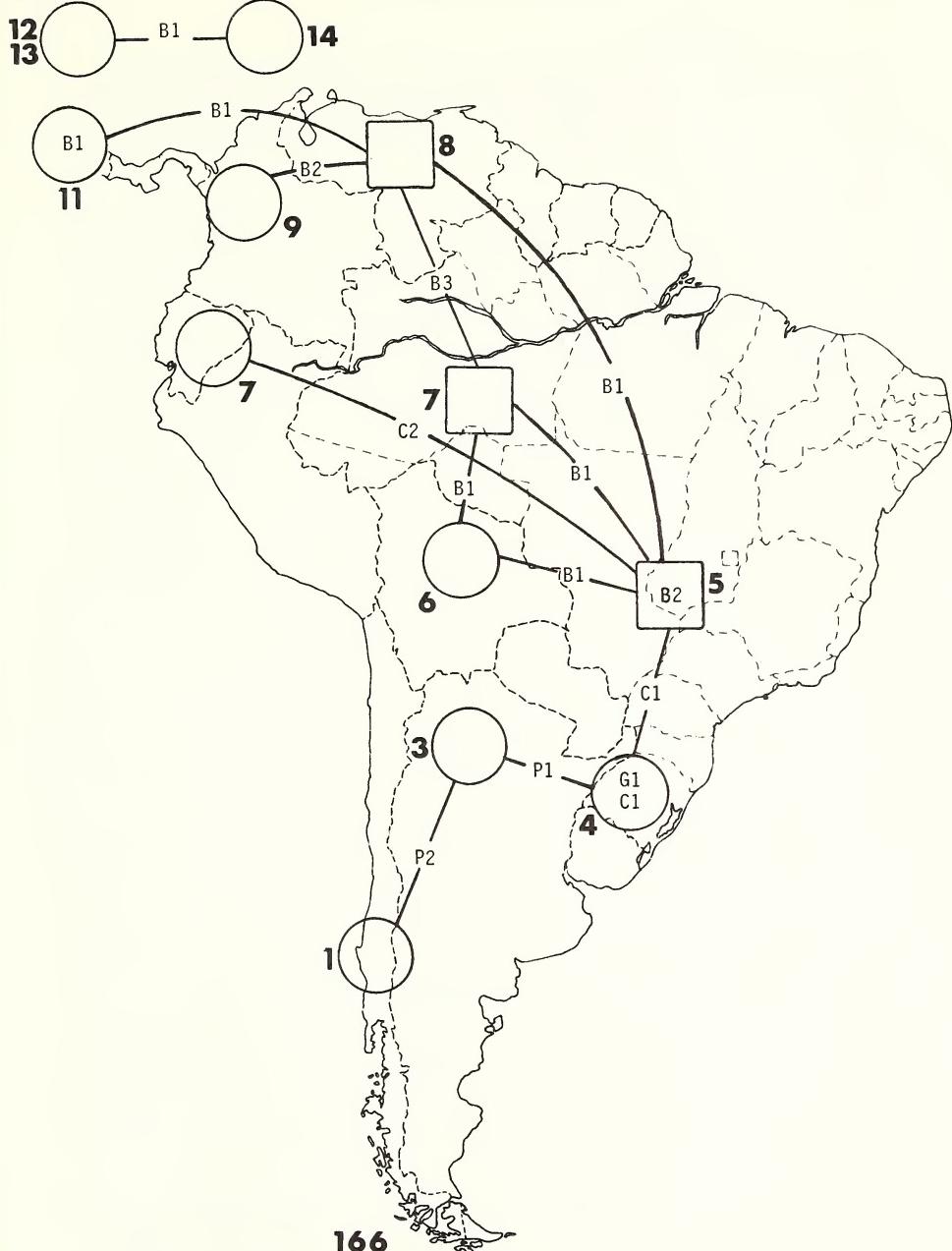
Fig. 166. Number of geographical relationships of allopatric sister lineages of *Brasiella, Gaymara, Plectographa* and *Cylindera*. Symbols: the number beside a circle denotes the geographical area; squares and circles are major and minor centres of species diversification respectively in designated geographical areas; letters denote subgenus; number beside letters denotes number of allopatric sister lineages, within (inside circles) or between (outside circle) geographical areas.

throughout the southern part of the Amazon basin during the last glacial episode, and its vicariance pattern recently caused by the spread of rainforest in the basin resulting in two allopatric populations, one in Ecuador and another in eastern Brazil.

Summary

Origins of the four studied subgenera were in western Gondwana prior to the formation of South America, and subsequent Neotropical diversification within subgenera took place mainly in the northern half of South America.

Major centers of species concentration, or refugia, of *Brasiella*, *Gaymara* and *Cylindera* are in eastern Brazil south of the Amazon River basin and that of *Plectographa* in northern Argentina. These centers have been long standing, perhaps for the entire Cenozoic Era, given their mix of related and unrelated taxa of different phylogenetic age. They were the chief sources of dispersal during hospitable climatic and geophysical episodes, and into which taxa retreated during the hostile episodes.

Major barriers over or through which taxa periodically passed, became geographically isolated and diversified, include the Amazon basin, Andes in Chile and Colombia, and Tertiary Central America. At the present time members of many taxa pairs are found on opposite sides of any one of these barriers. Arid regions in central parts of northern Argentina, and Pleistocene marine ingressions in northeastern Argentina (Noonan, 1985) may have been barriers effective in the diversification process of *Plectographa* lineages.

Climatic reversals resulting in vegetational changes in the Amazon basin during the last half of the Tertiary and Pleistocene were a fundamental cause of taxa formation. Open country conditions developing in glacial periods allowed general expansions of ranges into the basin. Division, isolation, and diversification of populations occurred with the return of humid tropical forests during interglacial periods.

PROBLEMS AND PREDICTIONS

1. Definitive taxonomic positions of *C. stamatovi*, *C. halophila*, *C. mixtula*, *C. nigrovittata*, *C. malaris* and *C. granulipennis* will be partly or wholly resolved by careful examinations of external and genitalic characters, and the reassessment of character weights.

2. Subgenus *Brasiella* species for which genitalic structures are not yet known, will have the flagellum absent from the male genitalia and the oviduct sclerite will be replaced by a membrane in females. Similarly, *Plectographa* species will have an elongate tooth with or without spatulate apex in males and ventral sclerite with two elongate posterior projections in females. Subgenus *Cylindera* species will have the central plate absent from males and ventral sclerite with two anterior lobes and two posterior projections in females.

3. The relationships analysis of *Cylindera* lineages is incomplete in the context of their New World history. Some South and North American taxa appear more closely related than we earlier suspected. This may be so for other groups not currently recognized as part of the *Cylindera* complex. One example is North American subgenus *Dromochorus* Guérin, the adults of which have a general habitus remarkably similar to those of the *morio* group.

4. This biogeography will change with changes in the reconstructed phylogeny or by geographical range extensions. The latter is likely to occur as new collections of specimens are made for taxa in areas peripheral to and within western parts of the Amazon basin. Until now that region has not been well collected, and what appear to be disjunct distributions may turn out to be more or less continuous geographical ranges. Candidates for range changes are *C. misella*, *C. dolosula* and *C. piligera*, among others.

5. Additional species of subgenus *Brasiella* that may be discovered will be in the New World, and mainly from eastern Brazil.

6. Additional species of subgenus *Gaymara* will be South American from southeastern Brazil.

7. Additional species of subgenus *Plectographa* will be from northern Argentina.

8. Additional South American species of *Cylindera* will be from eastern Brazil and the Amazon River basin.

9. It is evident that most species are closely associated with unforested regions. Many related taxa are divided by humid forests, particularly those of Amazonia. Dispersal routes followed by ancestors of these disjunct taxa have not been identified in our study. We do know that humid forests periodically gave way to grasslands and open country, but we do not know where they developed, and if there existed major and minor dispersal routes. In Webb's (1978) review of South American history of savanna vertebrates two major north-south routes are discussed, the Andes, "high road", and the Amazon basin "low road". Both routes were followed by non-forest vertebrate species. Taxa of *Brasiella* and *Cylindera* appear to form a composite geographical distribution pattern that coincides with the "low road". It extends from Colombia to southeastern Brazil through the western central and southern areas of the Amazon basin. Collections in western Brazil, Bolivia, Peru, and Ecuador will add distributional evidence in support of the Amazonian route for South American taxa of *Cicindela*.

ACKNOWLEDGEMENTS

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INDEX TO NAMES OF TAXA
(Synonyms in italics)

BOOK REVIEW

SCHWALM, F. E. 1988. Insect Morphogenesis. S. Karger AG, Basel. xix + 356 pp., 94 figs., 14 tables, subject index. $ 261.00 CAN!

Among the most active research areas in Biology today is that dedicated to understanding how genes control embryonic development in animals. Although progress towards achieving this goal has been phenomenal this past decade, principally because of the imaginative use of genetic engineering techniques, it has resulted from intensive study of less than a dozen, easy-to-maintain, "lab animals": the nematode, *Caenorhabditis elegans,* a few sea urchin and annelid species, the amphibian *Xenopus laevis, Drosophila melanogaster,* and the house mouse, *Mus musculus.* Not the least among the dangers of such narrow focus is production of a generation of biologists expert in the burgeoning techniques of molecular biology but unable to teach development from a comparative viewpoint and only at the lowest levels of biological organization. These levels are remote from the personal experience of most students and inaccessible to the senses but for 'laboratories' of high tech equipment. Also, it can be argued (e.g. Bartholomew, l986. Bioscience 36: 324-329) that to ask *incisive* questions about any aspect of its life, we must know the phylogenetic position of the animal being studied and have knowledge of higher levels in its organization particularly those concerning the whole animal and how it lives. Thus, is there still a place for a 'comparative embryology' such as this volume by Fritz Schwalm.

The book contains a preface by Friedrich Seidel (the "father" of experimental insect embryology), an introduction (3 pp.) and eight chapters concerning, respectively: systematics (4 pp.), imaginal morphology (17 pp.), gametogenesis and sex determination (63 pp.), insect culture and egg collecting techniques (13 pp.), oviposition and parental care (7 pp.), mating, egg structure and fertilization (19 pp.), tables of embryonic development (12 pp.) and a concluding chapter (at 147 pp., the "meat" of the book) on the structural aspects of insect embryogenesis.

In his preface, Seidel summarizes some high points in the early experimental study of insect embryos, emphasizing particularly results from his laboratory in the 1920's that demonstrated the existence of three physiological centres whose activity was required for normal blastoderm (the cleavage centre) and germ anlage formation (the activation centre) and for subsequent differentiation (the differentiation centre) of damselfly (*Platycnemis pennipes*) embryos. In addition, he comments at some length on the negative impact that evolutionary thinking has had on progress in experimental embryology and lauds Schwalm for writing "a monograph on 'pure' morphology" devoid of evolutionary speculation. Chief among the 'destructive' contributions he mentions is Ernst Haeckel's [1866] 'Biogenetic Law' (i. e. "Ontogeny recapitulates phylogeny"), pervasive in the late 19th and early 20th centuries, which suggested that since phylogeny was the "cause" of ontogeny, its experimental analysis was unnecessary. Because of his stature at that time in the

European scientific community, Haeckel was successful for some years in preventing such analysis from beginning. (Haeckel also postulated the existence of an hypothetical ancestral taxon, the "Gastraea" whose adult stage was never found despite numerous attempts to do so and which was thought to be recapitulated in the ontogeny of many modern animals as the *gastrula*). Seidel considers the primary contribution of developmental morphology to be provision of a structural basis for experimental study and implies that use of developmental information to establish homology of structure and to reconstruct phylogeny is of minor importance. The many biologists to-day (*e.g.,* Alberch, Bonner, Gould, Nelson, Smith, etc.) who are attempting to re-introduce consideration of ontogeny into evolutionary thinking, would disagree.

Seidel also discusses the concept of the "Korpergrundgestalt" or *basic body pattern*: an embryonic stage in the development of an animal that clearly identifies the higher level taxon to which that animal belongs. Members of a monophyletic lineage not only express their common phylogenetic origin in an easy to see way for the first time at this stage but diversify from it with subsequent development. For most hexapods, this stage is the "polypod" embryo: a fully segmented form usually bearing paired appendages on most of its body segments. Species as distantly related as bristle tails, mayflies, cockroaches and beetles pass through i' on their way to hatching. (One should not confuse this concept with the "(·ound Plan" of phylogenetic systematists which constitutes the collective, ancestr. ι character states of a taxon).

In his introduction, Schwalm refers briefly to some of the recent, illuminating, experimental work on regulatory genes now being carried out in *Drosophila* embryos: specifically the 'segmentation' genes whose normal expression results in determination of blastoderm cells to organise into a repeating series of homologous, segment primordia and the 'homoeotic' genes which specify segment identity and position. He recalls too E. B. Lewis' idea that the mesothorax is the '*basic body segment*' or "segment grundgestalt" upon which products of the homoeotic genes work to generate the diverse insect segments we now see.

Schwalm's objectives in writing the book were to: "...present embryonic morphogenesis in a sequence of 'typical' events which interdigitate with earlier and later events as the embryo forms..." and to identify differences in development among insects that are worthy of further analysis. He is reasonably successful in achieving these goals.

His chapters on systematics and adult morphology were obviously written by one who has little knowledge of or interest in either since they are poorly done and are not referred to again. Chapter 1 includes two cladograms revised from the works of Hennig, Kastner and Kristensen that can be used by the reader to organise the observations presented elsewhere in the book within an evolutionary framework. He considers the entognathous apterygotes (Collembola, Protura, Diplura) to be monophyletic and to constitute the sister group of the remaining insects; not to be

separate classes as many recent authors (e.g. Jamieson, Manton) have suggested. Chapter 2 contains some appropriate, though superficial, information on male and female reproductive systems and genitalia, but its brief summaries of distribution and behavioural adaptations seem totally out of place in a book on embryogenesis. He offers nothing about the role of sexual selection in shaping insect genitalia (see Eberhard, 1985. *Sexual Selection and Animal Genitalia*. Harvard).

In Chapter 3 are brief but reasonably up-to-date summaries of sex determination, hermaphroditism, parthenogenesis, heterogony and viviparity, oogenesis and egg membranes, spermatogenesis, sex ratios, life cycles and metamorphosis, neoteny, paedogenesis, caste formation in social insects, and quiescence and diapause. Coverage of comparative aspects is encyclopaedic and is presented in tables that include appropriate literature citations: Table I (6 pp.): oogenesis; II (2 pp.): synthetic activities of oocyte nuclei; III (2 pp.): types of parthenogenesis; IV (1 p.): sex ratios in Hymenoptera; and V (4 pp.): fecundity and duration of developmental stages.

Rearing and egg collecting methods are described in Chapter 4 for 69 species in 16 orders (Archaeognatha-2 spp., Zygentoma-2, Ephemeroptera-3, Odonata-10, Plecoptera-1, Phasmatodea-1, Orthoptera-6, Dictyoptera-2, Isoptera-2, Hemiptera-5, Coleoptera-11, Hymenoptera-6, Trichoptera-1, Lepidoptera-6, Mecoptera-1, and Diptera-11) and should be useful to investigators seeking for research beasts other than *Drosophila* upon which to work.

A straight, descriptive account of oviposition and egg masses in Chapter 5 informs us that Collembola "...deposit about 250 eggs in batches..." and that "... Psocoptera lay individual eggs or form cocoons with egg batches...". Schwalm seems not to realise that individual females, not taxa, deposit eggs. Generalizations such as these are of little value since they are based on detailed knowledge of a few species whose identities are only sporadically revealed.

Mating behaviour, and the size (Table VI: 3 pp.), shape, maturation, internal structure and fertilization of eggs are discussed in Chapter 6 while tables of embryogenic development comprise Chapter 7: Table VII (6 pp.): the literature of descriptive embryogenesis arranged by order and VIII (4 pp.): timetables for major morphogenetic events in the embryogenesis of 52 species in 18 orders (Collembola-1 sp., Archaeognatha-2, Zygentoma-1, Ephemeroptera-1, Odonata-1, Plecoptera-1, Phasmida-1, Orthoptera-5, Dictyoptera-3, Isoptera-1, Hemiptera-4, Coleoptera-6, Megaloptera-1, Neuroptera-1, Hymenoptera-6, Trichoptera-1, Lepidoptera-10 and Diptera-4) . Both tables are filled with information that would require much effort to extract from the primary literature.

The final chapter is a detailed, well illustrated summary of embryonic development beginning with cleavage and ending with hatching. Coverage is extensive and up-to-date and on insects selected from throughout the class. Only very recent discoveries are not mentioned (*e.g.,* Ball and Goodman's [1983, 1985] ingenious experimental work on muscle pioneers in locust embryos [Nature 301:

66-69; Dev. Biol. 111: 383-418], Campos-Ortega and Hartenstein's [1985] superb book on the embryogenesis of *Drosophila* and recent papers on the embryogenesis of Thysanoptera [Heming, 1979. J. Morph. 160: 323-344; 1980. *Ibid.* 164: 235-263; Haga, 1985. Rec. Adv. Ins. Embryol. Jap. 1: 45-106; and Moritz, 1988. Zool. Jb. Anat. 117: 1-64]). The book contains 1255 references of which 156 were published after 1980.

Much comparative information is, again, presented in tables: Table IX (4 pp.): duration of nuclear cycles during cleavage; X (1 p.): vitellophage fate; XI (1 p.): pole cell formation; XII (1 p.): intercalary appendages; XIII (1 p.): head segmentation; and XIV (1 p.): embryonic abdominal appendages and their fate.

The book is nicely printed on good quality paper and seems to be strongly bound but is exorbitantly priced and has numerous typographical errors and a substantial number of errors in interpretation. In his preface, Seidel hopes "...that the volume will find wide distribution and that it will generate new developmental concepts for experimental analysis" (p. xvi). At $ 261.00 (CAN) this is hardly possible since only the most pecunious of libraries and individuals will be able to afford it. Also, much of its content is better presented in other works that are readily available in most libraries (*e.g.,* Anderson, 1973. *Embryology and Phylogeny in Annelids and Arthropods,* Pergamon Press; Counce and Waddington [eds.], 1972, 1973. *Developmental Systems: Insects,* Vols. 1 & 2, Academic Press; Haget, 1977. *Traité de Zoologie,* Vol. 8, part 5Ba: 1-262; 279-387. Masson et Cie; and Sander, Gutzeit and Jackle, 1985. pp. 319-385 *In* Kerkut and Gilbert [eds.] *Comparative Insect Physiology, Biochemistry and Pharmacology.* Vol. 1. Pergamon Press).

Below I note some of the more obvious errors in interpretation:

p. viii: insects do *not* constitute a phylum;

p. 14: the Devonian formations he refers to are 375–400 million years old *not* 350;

p. 20: the Monarch Butterfly, *Danaus plexippus*, is a new world species;

p. 46: Thysanoptera are *not* known to have nonparthenogenetic paedogenesis. Rather males of the thripid, *Limothri₁   lenticornis* develop more rapidly than females, are preferentially attracted to an   ate with female pupae and lodge fully differentiated spermatozoa in their still un. nished spermathecae (Bournier, 1956. Arch. Zool. exp. gen. 93: 219-317);

Tables I, III, V, X: numerous misplacements of genera or the laboratory species of various authors into families and higher taxa;

p. 73: adult aphid macropterae usually develop in crowded conditions not the opposite;

p. 230: the pleuropodia of the phasmid, *Carausius* develop from modifications in the embryonic appendages of abdominal segment 1 (ectodermal), as in many other insects, *not* from secondary coelomic sacs (mesodermal) (Louvet. 1976. Int. J. Ins. Embryol. Morphol. 5: 35-49);

p. 238: Some neuroblasts rather than degenerating towards the end of embryogenesis in holometabolous embryos, persist and divide teloblastically again during larval development, eventually to generate large numbers of imaginal neurons which differentiate during metamorphosis (Heming [1982] J. Morphol. 172: 23-43; Booker and Truman [1987] J. Comp. Neurol. 255: 547-559; Truman and Bate [1988] Dev. Biol. 125: 145-157.);

p. 254: the description of mouthpart morphogenesis in thrips is derived from Risler's (1956) account of *adult* mouthparts in *Thrips physapus*. A full description of their *embryonic* development in *Haplothrips verbasci* is presented by Heming (1980. J. Morphol. 164: 235-263).

p. 255: labels for labial palpus and paraglossa are incorrect in Fig. 85c;

p. 257: salivary gland invaginations in *Drosophila* are here said to originate between the labial and prothoracic segments; in Fig. 86c, they are shown as being located between the maxillary and labial segments.

Finally, there are numerous inconsistencies in the use of subtitles and some of his paragraphs go on for pages. Considering the above, one is better advised to purchase one of the general references cited above.

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Quaestiones

Entomologicae

A periodical record of entomological investigations,
published at the Department of Entomology,
University of Alberta, Edmonton, Canada.

CONTENTS

CONTENTS

SYSTEMATIC STUDIES ON PSEUDOMYRMECINE ANTS: REVISION OF THE *PSEUDOMYRMEX OCULATUS* AND *P. SUBTILISSIMUS* SPECIES GROUPS, WITH TAXONOMIC COMMENTS ON OTHER SPECIES

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ABSTRACT

*The first part of this paper contains a synopsis of the major species groups and revisions of two such groups (*P. oculatus *group,* P. subtilissimus *group) in the large Neotropical ant genus* Pseudomyrmex. *Eleven species are recognized in the* P. oculatus *group, of which three are new:* P. alustratus *Ward (from Peru),* P. cretus *Ward (Costa Rica), and* P. pisinnus *Ward (Brazil).* P. caeciliae *(Forel) is raised to species* (stat. nov.), *and the following new synonymy is proposed:* P. elongatus *(Mayr)* = P. alliodorae *(Wheeler);* P. oculatus *(F. Smith)* = P. altinodus *(Mann)* = P. tuberculatus *(Enzmann)* = P. wessoni *(Enzmann);* P. urbanus *(F. Smith)* = P. chodati *(Forel)* = P. ogloblini *(Santschi). Four species are recognized in the* P. subtilissimus *group of which two are new:* P. spiculus *Ward (Costa Rica), and* P. villosus *Ward (Brazil).* P. culmicola *(Forel) is proposed as a junior synonym of* P. tenuissimus *(Emery). A final section of the paper contains taxonomic comments, including new synonymy and lectotype designations, on 22 other species of* Pseudomyrmex, *in various species groups, with emphasis on taxa which are associated with ant-plants. No new species are described but three taxa [*P. pazosi *(Santschi),* P. rufiventris *(Forel), and* P. tachigaliae *(Forel)] are raised to species (*stat. nov.*); two species [*P. dendroicus *(Forel),* P. osurus *(Forel)] are removed from synonymy (*stat. reval.*); a replacement name (*P. laevifrons *Ward, nom. nov.) is provided for* P. laeviceps *(F. Smith), 1877 (nec F. Smith, 1859); and 32 new synonymies are proposed. Identities of some of the* Pseudomyrmex *species inhabiting* Acacia, Tachigali, *and* Triplaris *are clarified.*

RÉSUMÉ

La première partie de cet travail contient un sommaire des groupes principaux d'espèces et révisions de deux tels groupes (groupe P. oculatus, *groupe* P. subtilissimus) *dans le grand genre Neotropicaux,* Pseudomyrmex. *Onze espèces sont reconnues dans le groupe* P. oculatus, *desquelles trois sont nouvelles:* P. alustratus *Ward (de Peru),* P. cretus *Ward (Costa Rica), et* P. pisinnus *Ward (Brazil).* P. caeciliae *(Forel) est élevé à l'étage d'espèce (stat. nov.) et le nouveau synonymie suivant est proposé:* P. elongatus *(Mayr)* = P. elongatus *(Wheeler);* P. oculatus *(F. Smith)* = P. altinodus *(Mann)* = P. tuberculatus *(Enzmann)* = P. wessoni *(Enzmann);* P. urbanus *(F. Smith)* = P. chodati *(Forel)* = P. ogloblini *(Santschi). Quatre espèces*

sont reconnues dans le groupe P. subtilissimus, *desquelles deux sont nouvelles:* P. spiculus Ward *(Costa Rica), et* P. villosus Ward *(Brazil).* P. culmicola *(Forel) est proposé comme un nouveau synonyme de* P. tenuissimus *(Emery). Une section finale contient notes taxonomiques, comprenant nouveau synonymie et désignation des lectotypes, sur 22 autres espèces de* Pseudomyrmex, *dans quelques groupes d'espèces, avec accent sur taxa qui sont associés avec des plantes myrmecophiles. On ne decrit pas nouvelles espèces, mais trois taxa [P.* pazosi *(Santschi),* P. rufiventris *(Forel), et* P. tachigaliae *(Forel)] sont elevés au niveau d'espèce* (stat. nov.); *deux espèces [P.* dendroicus *(Forel),* P. osurus *(Forel)] sont enlevés de synonymie* (stat. reval.); *un nom de remplacement (P.* laevifrons Ward, *nom. nov.) est fourni pour* P. laeviceps *(F. Smith), 1877 (nec F. Smith, 1859); et 32 nouveaux synonymes sont proposés. Les identités de quelques espèces de* Pseudomyrmex *qui vivent dans* Acacia, Tachigali *et* Triplaris *sont clarifiées.*

TABLE OF CONTENTS

INTRODUCTION

The New World ant genus *Pseudomyrmex* contains a large number of species and is a conspicuous element of the Neotropical arboreal ant fauna. It is known from

southern United States (with northward extensions to about 40°N latitude on the east and west coasts) south to approximately 36°S in Chile and Argentina. A closely related Old World genus, *Tetraponera*, is distributed from Africa to southeastern Asia and Australia. Much taxonomic work remains to be done on these ants, both in terms of species diagnosis and phylogenetic evaluation. Within the genus *Pseudomyrmex* there are more than 250 available species-level names, of which about 70% are valid presently. Most of these names accumulated in a piece-meal fashion in the late nineteenth and early twentieth centuries, without the benefit of any synthetic, revisionary studies. As a first attempt to deal with the taxonomy of this genus, Kempf (1958, 1960, 1961, 1967) delineated five species groups, containing about half of the described taxa, and clarified the identities of some species within these groups. The Nearctic species of *Pseudomyrmex* were reviewed by Ward (1985), who recognized two additional species groups (*P. elongatus* group, *P. pallidus* group).

The present paper contains a reevaluation and synopsis of the major species groups, and revisions of two such groups: (i) the *P. oculatus* group, which is expanded to include the "*elongatus* group" of Ward (1985), and (ii) the *P. subtilissimus* group, here defined and diagnosed for the first time. A fourth section contains taxonomic comments about some of the remaining species of *Pseudomyrmex*. It is based on a study of type material in European and North American collections, and helps to provide a foundation for future revisionary work on the other major species groups. Such work, currently in progress, will include keys to species groups and to isolated species of uncertain placement, as well as phylogenetic assessments of the relationships among groups. A preliminary analysis of these relationships is presented in Ward (1990a). A generic revision of the subfamily Pseudomyrmecinae and a higher-level phylogenetic analysis appears in Ward (1990b).

The genus *Pseudomyrmex* is richly endowed with sympatric sibling species and taxonomically confusing "species complexes", a situation which is apparent even in the depauperate Nearctic fauna (Ward, 1985). The resolution of such taxonomic imbroglios requires careful analysis of character variation in large samples of diverse geographic origins. *Pseudomyrmex* workers do not exhibit striking interspecific variation in sculpture or spinescence; differences between closely related species often reside in subtle contrasts of size and shape. I have attempted to quantify these differences wherever practical and to avoid subjective qualitative statements. But quantitative assessments of size and shape often reveal an impressive amount of apparent intraspecific variation, making the search for diagnostic differences challenging. Needless to say, precise metric measurements are necessary for the accurate determination of many *Pseudomyrmex* species, and the taxa dealt with in this paper are no exception.

MATERIALS AND METHODS

Collections

Material was examined in the following collections (abbreviations follow those of Arnett & Samuelson (1986) as closely as possible):

BMNH   British Museum (Natural History), London, U.K.

CASC   California Academy of Sciences, San Francisco, CA, USA

CDAE   California Dept. of Food and Agriculture, Sacramento, CA, USA

CELM   Colección Entomología "Luis Maria Murillo", Instituto Colombiano Agropêcuario, Bogotá, Colombia

CISC   California Insect Survey, University of California at Berkeley, CA, USA

CKIC   C. Kugler Collection, Radford University, VA, USA

CNCC   Canadian National Collection of Insects, Biosystematics Research Institute, Ottawa, Canada

CUIC   Cornell University Insect Collection, Ithaca, NY, USA

EBCC   Estación de Biología Chamela, Jalisco, Mexico

FFIC   Fernando Fernández Collection, Bogotá, Colombia

GBFM   Graham B. Fairchild Museo de Invertebrados, Universidad de Panama, Panama

GCWC   G. C. & J. Wheeler Collection, Silver Springs, FL, USA

GHPC   G. H. Perrault Collection, Paris, France

ICCM   Carnegie Museum of Natural History, Pittsburg, PA, USA

IEGG   Istituto di Entomologia "Guido Grandi", Università de Bologna, Italy

INHS   Illinois Natural History Survey Insect Collection, Champaign, IL, USA

INPA   Instituto Nacional de Pesquisas da Amazonia, Manaus, Brazil

IZAV   Instituto de Zoología Agrícola Universidad Central de Venezuela, Maracay, Venezuela.

JTLC   J. T. Longino Collection, University of California at Santa Barbara, CA, USA

KSUC   Kansas State University Insect Collection, Manhattan, KS, USA

KWJC   K. W. Jaffé Collection, Universidad Simon Bolívar, Caracas, Venezuela

LACM   Los Angeles County Museum of Natural History, Los Angeles, CA, USA

MCSN   Museo Civico di Storia Naturale, Genoa, Italy

MCZC   Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA

MHNG   Muséum d'Historie Naturelle, Geneva, Switzerland

MJPL   Museo de Historia Natural "Javier Prado", Lima, Peru

MNCR   Museo Nacional de Costa Rica, San José, Costa Rica

MNHN   Muséum National d'Histoire Naturelle, Paris, France

MZSP   Museo de Zoologia da Universidade de São Paulo, Brazil

NHMB   Naturhistorisches Museum, Basel, Switzerland

NHMV   Naturhistorisches Museum, Vienna, Austria

NHRS Naturhistoriska Riksmuseet, Stockholm, Sweden

OSUO Department of Entomology Collection, Oregon State University, Corvallis, OR, USA

PSWC P. S. Ward Collection, University of California at Davis, CA, USA

SEMC Snow Entomological Museum, University of Kansas, Lawrence, KS, USA

TAMU Department of Entomology Insect Collection, Texas A&M University, College Station, TX, USA

UCDC Bohart Museum of Entomology, University of California at Davis, CA, USA

UCRC UCR Entomological Collection, University of California at Riverside, CA, USA

UNCB Museo de Historia Natural, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia

USNM National Museum of Natural History, Washington, DC, USA

UWEM Entomology Museum, University of Wisconsin, Madison, USA

WPMC W. P. MacKay Collection, College Station, TX, USA

WWBC W. W. Benson Collection, Campinas, SP, Brazil

ZMHB Zoologisches Museum, Museum für Naturkunde der Humboldt - Universität, Berlin, East Germany

ZMUC Zoologisk Museum, University of Copenhagen, Dennmark

ZMUH Zoologisches Institut und Zoologisches Museum, Universität Hamburg, West Germany

ZSMC Zoologische Sammlung des Bayerischen Staates, Munich, West Germany

Metric Measurements and Indices

Metric measurements were made at 50X power on a Wild microscope, with a dual-axis (X-Y) pair of Nikon micrometers wired to an Autometronics digital readout. All measurements were taken to the nearest thousandth of a millimeter. Most have been rounded to two decimal places for presentation here.

Some of the measurements described below differ from those used in taxonomic studies of other ants. These modifications are partly dictated by peculiarities of the Pseudomyrmecinae. For example, following Kempf (1960), the compound eyes are included in the measurement of head width in workers and queens (as well as males), because the maximum width of the head capsule frequently occurs behind the eyes and is blocked from view. In addition I use DPL (diagonal length of the propodeum; see below) as a proportional measure of mesosoma (=alitrunk) length rather than WL (Weber's length of the entire mesosoma) because the free articulation of the pronotum with the rest of the thorax renders the measurement of WL imprecise.

A number of important measurements are taken with the head in a full-face, frontal (*i.e.,* dorsal) view. To make such measurements comparable among all

pseudomyrmecine ants, the head is positioned so that its anterolateral margins (above the mandibular insertions) are in the same focal plane as the occipital margin (see Fig. 6). The head length (HL) which is measured in such a view includes the median clypeal lobe, but the axis of measurement is not unduly altered by a strong anterodorsal protrusion of the fronto-clypeal complex as occurs, for example, in some *Tetraponera*. As a result, HL is slightly less than the "maximum critical" head length (Brown, 1953), but it and other measurements which are taken in a full-face view of the head are more appropriate for comparisons across the entire subfamily.

For *Pseudomyrmex* workers and queens a full-face, frontal view of the head is roughly equivalent to positioning the median ocellus and the frontal carinae in the same plane of view (while turning the head so that the maximum possible head width is achieved). Such a positioning rule does not usually work in *Tetraponera*, due to discrepancies in head shape and the frequent lack of ocelli in workers.

In discussions below, the *antennal sclerite* is the sclerite which encircles the antennal fossa. In most ants, the inner margin of the antennal sclerite is developed as a *median lobe* (Fig. 3) which is raised dorsolaterally and often covers part of the basal condyle of the antenna. In pseudomyrmecine ants these same median lobes typically fuse with the frontal carinae anteromedially (Fig. 3); in many other ants the frontal carinae are themselves expanded laterally to form frontal lobes which cover the median lobes of the antennal sclerites.

The following is a list of measurements used in this and other continuing studies of pseudomyrmecine ants. Explanatory illustrations of some of these measurements are found in Ward (1985); see also Figs. 1–5 of this paper.

HW   Head width: maximum width of head, including the eyes, measured in full-face dorsal view.

VW   Vertex width: width of the posterior portion of the head (vertex), measured along a line drawn through the lateral ocelli, with the head in full-face, dorsal view (see Fig. 1 in Ward [1985]).

HL   Head length: midline length of head proper, measured in full-face, dorsal view, from the anterior clypeal margin to the midpoint of a line drawn across the occipital margin.

EL   Eye length: length of compound eye, measured with the head in full-face, dorsal view.

OD   Ocellar distance: distance from the middle of the median ocellus to the midpoint of a line drawn between the lateral ocelli, measured with the head in full-face dorsal view (see Fig. 1 in Ward [1985]).

OOD   Oculo-ocellar distance: distance from the middle of the median ocellus to the midpoint of a line drawn across the posterior margins of the compound eyes, measured with the head in full-face, dorsal view (see Fig. 1 in Ward [1985]) (this distance is negative in value if the posterior margin of the compound eye exceeds the median ocellus).

CD   Clypeal distance: distance from the anterior clypeal margin to the midpoint of a line drawn across the anterior margins of the antennal sclerites.

MD1-

MD9   A series of mandibular measurements (see Figs. 1, 2) taken with the mandibles removed from their insertions and mounted separately on a point. For measurements of width and overall length (MD1 - MD3), the mandible is positioned so that the dorsal abductor swelling and the apical tooth are in the same focal plane (Fig. 2) and it is then rotated on this axis until MD2, the width of the mandible at the juncture of the basal and masticatory margins, is made maximum. Measurements of the lengths of the basal and masticatory margins, and of the relative positioning of teeth along those margins (MD4 - MD9), are taken with the extreme ends of the respective margin in the same focal plane. If there is more than one mesial basal tooth, MD4 is the distance to the outermost one.

MFC   Minimum frontal carinal distance: minimum distance between the frontal carinae, posterior to their fusion with, or approximation to, the antennal sclerites (Fig. 4).

ASD   Antennal sclerite distance: maximum distance between the lateral margins of the median lobes of the antennal sclerites, measured in full-face, dorsal view of the head (Fig. 4).

ASO   Antennal sclerite distance, outer margins: maximum distance between the outer, lateral margins of the antennal sclerites (Fig. 4).

EW   Eye width: maximum width of compound eye, measured along its short axis, in an oblique dorso-lateral view of the head.

EL2   Eye length: maximum length of compound eye, measured along its long axis in the same plane of view as EW.

SL   Scape length: length of the first antennal segment, excluding the radicle.

LF1   Length of first funicular segment: maximum measurable length of the first funicular segment (pedicel), including its basal articulation in workers and queens but excluding the basal articulation in males (where it is usually hidden).

LF2   Length of second funicular segment: maximum measurable length of the second funicular segment.

LF3   Length of third funicular segment: maximum measurable length of the third funicular segment.

WF2   Width of second funicular segment.

FL   Fore femur length: length of the fore femur, measured along its long axis in posterior view (see Fig. 3 in Ward [1985]).

FW   Fore femur width: maximum measurable width of the fore femur, measured from the same view as FL, at right angles to the line of measurement of FL.

DPL   Diagonal length of the propodeum: length of the propodeum, measured in lateral view along a diagonal line drawn from the "metapleural" lobe to the metanotal groove (see Fig. 2 in Ward (1985)).

BF   Length of the basal (=dorsal) face of the propodeum, measured in lateral view from the metanotal groove to the point on the surface of the propodeum which is maximally distant from the diagonal propodeal line.

DF   Length of the declivitous face of the propodeum, measured in lateral view from the metapleural lobe to the point on the surface of the propodeum which is maximally distant from the diagonal propodeal line.

MP   Depth of metanotal groove ("mesopropodeal impression"), measured in lateral view from the bottom of the metanotal groove to a line drawn across the dorsal surface of the mesonotum and propodeum.

PL   Petiole length: length of the petiole, measured in lateral view from the lateral flanges of the anterior peduncle to the posterior margin of the petiole (see Fig. 4 in Ward [1985]).

PND   Petiolar node distance: distance from the lateral flanges of the anterior petiolar peduncle to the maximum height of the node, measured from the same view as PL and along the same line of measurement (see Fig. 4 in Ward [1985]).

PH   Petiole height: maximum height of the petiole, measured in lateral view at right angles to PL, but excluding the anteroventral process.

PPL   Postpetiole length: length of the postpetiole, measured in lateral view, from the anterior peduncle (of the postpetiole) to the point of contact with the fourth abdominal tergite, excluding the pretergite (see Fig. 4 in Ward [1985]).

DPW   Dorsal petiolar width: maximum width of the petiole, measured in dorsal view.

MPW   Minimum petiolar width: minimum width of the petiole, measured in dorsal view, anterior to DPW.

PPW   Dorsal postpetiolar width: maximum width of the postpetiole, measured in dorsal view.

LHT   Length of hind tibia: maximum measurable length of hind tibia, excluding the proximal part of the articulation which is received into the distal end of the hind femur (Fig. 5).

LHS   Length of hind basitarsus: maximum measurable length of hind basitarsus.

Indices calculated from the preceding measurements include the following ratios (the orthodox but redundant and potentially misleading procedure of multiplying ratios by 100 has not been adopted):

CI   Cephalic index: HW/HL
OI   Ocular index: EW/EL
OI2   Ocular index, using EL2: EW/EL2
REL   Relative eye length: EL/HL
REL2   Relative eye length, using HW: EL/HW
OOI   Oculo-ocellar index: OOD/OD
VI   Vertex width index: VW/HW
FCI   Frontal carinal index: MFC/HW
FCI2   Frontal carinal index, using ASD: MFC/ASD
ASI   Antennal sclerite index: ASD/ASO
SI   Scape index: SL/HW
SI2   Scape index, using EL: SL/EL
FLI   Funicular length index: (LF2 + LF3)/WF2
FI   Fore femur index: FW/FL
PDI   Propodeal index: BF/DF
MPI   Metanotal index: MP/HW
NI   Petiole node index: PND/PL
PLI   Petiole length index: PH/PL
PLI2   Petiole length index, using PPL: PPL/PL
PWI   Petiole width index: DPW/PL
PWI2   Petiole width index, using PPW: DPW/PPW
PWI3   Petiole width index, using MPW: MPW/DPW
PPWI   Postpetiole width index: PPW/PPL
PPWI2   Postpetiole width index, using HW: PPW/HW

Other Conventions

Palp formula refers to the number of maxillary palp segments, followed by the number of labial palp segments. In counting the numbers of teeth on the basal and masticatory margins of the mandibles, the apico-basal tooth (see Fig. 1) is considered to be part of the dentition of the masticatory margin. The following setal counts are employed:

MSC   Mesosoma setal count: number of standing hairs, *i.e.,* those forming an angle of 45° or more with the cuticular surface (Wilson, 1955), visible in outline on the mesosoma dorsum in lateral view.
HTC   Hind tibial setal count: number of standing hairs visible in outline on the outer (extensor) surface of the hind tibia, with the line of view orthogonal to the plane of tibial flexion.
MTC   Mid tibial setal count: equivalent count for mid tibia.

Terms for surface sculpture follow Harris (1979). When material was examined under a light microscope, an opaque (Mylar) filter was placed between the source of

illumination and the specimen, at a distance of about 4 cm from the latter. The consequent reduction of glare renders the details of sculpture more visible, and permits greater discrimination between different degrees of reflectance of the integument. The terms opaque, subopaque, sublucid, and lucid are used to make distinctions along this continuum of reflectance, opaque indicating a lack of reflectance, on the one hand, and lucid referring to a strongly shining integument, on the other hand, *under the conditions of soft lighting described above.*

Scanning electron micrographs were taken with an ETEC Autoscan, using gold-palladium coated specimens.

The term *stat. nov.* is used for a change in status of a valid name (in all instances here: elevation from infraspecific to specific status), while *stat. reval.* refers to the revalidation of a name previously considered invalid (in all instances here: resurrection of a former synonym). The distinction between these two kinds of name changes was not made in Ward (1985).

In the lists of material examined, records are arranged alphabetically by country and by principal administrative region within larger countries. The abbreviations for Brazilian states follow Kempf (1972), with the following additions: MS = Mato Grosso do Sul; RR = Roraima.

The abbreviation "c.u." signifies collector unknown.

SYNOPSIS OF MAJOR SPECIES GROUPS IN *PSEUDOMYRMEX*

Among ants whose workers possess a distinct postpetiole and well-developed sting, those of *Pseudomyrmex* are recognized by their elongate compound eyes (OI 0.48–0.66, REL 0.36–0.68), closely set frontal carinae (FCI 0.01–0.13), and short scapes (SI 0.40–0.52). The median lobes of the antennal sclerites are also closely adjacent (ASI 0.41–0.73) and visible in a full-face view of the head. The antennae are 12-segmented. The mandibles are relatively small, with well differentiated basal and masticatory margins bearing 2–3 and 5–10 teeth, respectively.

Within the genus *Pseudomyrmex* I recognize currently nine major species groups, containing about 85% of the described taxa. The most salient worker characteristics of these groups are summarized in Table 1.

The outline of species groups is tentative, details of which undoubtedly will undergo refinement. The *pallens* group, in particular, appears to be rather heterogeneous and is probably paraphyletic. Additional undescribed species are in most of these groups; and there is a residue of taxonomically isolated species, and taxa of uncertain identity (*incertae sedis*). Nevertheless Table 1 should permit the assignment of most worker-based material of *Pseudomyrmex* to a species group.

The valid described taxa in each group are given below. All names are implicitly listed as binomina (since I expect all infraspecific names eventually either to enter synonymy or be raised to species), and the nomenclatural changes of this paper have been incorporated.

Table 1. Worker characteristics useful for distinguishing the major species groups of *Pseudomyrmex*. There are additional isolated taxa not belonging to these groups (see text).

Species group	Palp formula(e)	No. teeth on masticatory margin of mandibles[a]	Lateral corners of median clypeal lobe: rounded (or bluntly angled) versus sharply angulate	Pilosity on mesosoma dorsum: common (MSC>10) versus sparse (MSC<8)	Tibial pilosity: common ([HTC + MTC] >10) versus sparse ([HTC + MTC]<8)	Eye size: relatively short (REL 0.36–0.46) versus elongate (REL 0.48–0.68)	Other
gracilis	6,4	7–10	rounded[b]	common[c]	common[c]	elongate	pronotum laterally (sub)marginate
tenuis	6,4	6	rounded	sparse	sparse	elongate	metanotal groove lacking
sericeus	6,4;5,4	8–10	rounded	sparse	sparse	elongate	silky (sericeous) integument
pallens	6,4	5–6	rounded	usually sparse	sparse	variable	–
viduus	6,4;5,3;4,3	5–7	variable	common	common[d]	short	broad petiole (PWI > 0.70)
oculatus	6,3;5,3	5–6	rounded	common	usually sparse	elongate	protruding, tectiform median clypeal lobe
subtilissimus	6,3	5	rounded	sparse	sparse	elongate	frontal carinae not fusing with antennal sclerites
pallidus	5,3;4,3	5	angulate	sparse	sparse	variable	–
ferrugineus	5,3;4,3	6	variable	common	sparse	short	inhabiting swollen-thorn *Acacia*

[a] Median number of teeth within a nest-series; occasional deviations occur
[b] Somewhat angulate in *P. laevigatus* (F. Smith)
[c] Except *P. simulans* Kempf
[d] Except *P. tachigaliae* (Forel)
"No." = Number

P. ferrugineus group

alfari (Forel), atrox (Forel), bicinctus (Santschi), ferrugineus (F. Smith), flavicornis (F. Smith), gaigei (Forel), infernalis (Wheeler), nigrocinctus (Emery), peltatus (Menozzi), peperi (Forel), scelerosus (Wheeler), spinicola (Emery), veneficus (Wheeler).

P. gracilis group

alternans (Santschi), alvarengai Kempf, argentinus (Santschi), atrinodus (Santschi), atripes (F. Smith), bicolor (Guérin), browni Kempf, canescens (F. Smith), cladoicus (F. Smith), dimidiatus (Roger), excisus (Mayr), faber (F. Smith), glabriventris (Santschi), godmani (Forel), gracilis (Fabricius), laevigatus (F. Smith), maculatus (F. Smith), major (Forel), mexicanus (Roger), niger (Donisthorpe), nigropilosus (Emery), osurus (Forel), pilosulus (F. Smith), pupa (Forel), sericatus (F. Smith), simulans Kempf, squamiferus (Emery), unicolor (F. Smith), velifer (Stitz), venustus (F. Smith), volatilis (F. Smith).

P. oculatus group

alustratus Ward, caeciliae (Forel), cretus Ward, cubaensis (Forel), curacaensis (Forel), eduardi (Forel), elongatus (Mayr), oculatus (F. Smith), pisinnus Ward, schuppi (Forel), urbanus (F. Smith).

P. pallens group

adustus (Borgmeier), apache Creighton, championi (Forel), elongatulus (Dalle Torre), gibbinotus (Forel), incurrens (Forel), landolti (Forel), longus (Forel), lynceus (Spinola), monochrous (Dalle Torre), pallens (Mayr), phyllophilus (F. Smith), salvini (Forel), thoracicus (Norton).

P. pallidus group

acanthobius (Emery), belgranoi (Santschi), brunneus (F. Smith), cocae (Santschi), colei (Enzmann), distinctus (F. Smith), ejectus (F. Smith), ethicus (Forel), euryblemma (Forel), fiebrigi (Forel), flavidulus (F. Smith), fuscatus (Emery), holmgreni (Wheeler), leptosus Ward, levivertex (Forel), lizeri (Santschi), pallidus (F. Smith), pazosi (Santschi), peruvianus (Wheeler), rochai (Forel), rufiventris (Forel), seminole Ward, simplex (F. Smith), solisi (Santschi), terminalis (F. Smith), virgo (Santschi), vistanus (Enzmann).

P. sericeus group

acaciarum (Wheeler), beccarii (Menozzi), castus (Wheeler), cordiae (Forel), fortis (Forel), heterogynus (Wheeler & Mann), huberi (Santschi), humboldi (Enzmann), ita (Forel), lisus (Enzmann), longior (Forel), pictus (Stitz), rubiginosus (Stitz), sericeus (Mayr), vinneni (Forel).

P. subtilissimus group

spiculus Ward, *subtilissimus* (Emery), *tenuissimus* (Emery), *villosus* Ward.

P. tenuis group

boopis (Roger), *denticollis* (Emery), *tenuis* (Fabricius), *termitarius* (F. Smith).

P. viduus group

concolor (F. Smith), *cordobensis* (Forel), *coronatus* (Wheeler), *dendroicus* (Forel), *endophytus* (Forel), *kuenckeli* (Emery), *malignus* (Wheeler), *nigrescens* (Forel), *opacior* (Forel), *rurrenabaquensis* (Wheeler & Mann), *symbioticus* (Forel), *tachigaliae* (Forel), *triplaridis* (Forel), *triplarinus* (Weddell), *viduus* (F. Smith).

Incertae sedis

antiguanus (Enzmann), *brunnipes* (Enzmann), *costaricensis* (Enzmann), *depressus* (Forel), *duckei* (Forel), *fervidus* (F. Smith), *filiformis* (Fabricius), *gebelli* (Forel), *goeldii* (Forel), *haytianus* (Forel), *laevifrons* Ward, *mandibularis* (Spinola), *oki* (Forel), *perboscii* (Guérin), *rufomedius* (F. Smith), *santschii* (Enzmann), *subater* (Wheeler & Mann), *voytowskii* (Enzmann), *weberi* (Enzmann), *wheeleri* (Enzmann).

TAXONOMIC TREATMENT OF *PSEUDOMYRMEX OCULATUS* AND *SUBTILISSIMUS* GROUPS

PSEUDOMYRMEX OCULATUS GROUP

Introduction

Diagnosis (worker).— Small to medium-size species (HW 0.47–0.98), head longer than broad, often markedly so (CI 0.61–0.88), with medium to large eyes (REL 0.48–0.61); mandibles with external and basal margins parallel or diverging slightly (MD1/MD2 0.87–1.00); basal margin of mandibles with a single distal tooth, masticatory margin with five or (less commonly) six teeth; frontal carinae subcontiguous (FCI 0.017–0.047), fusing anterolaterally with the antennal sclerites, so that in lateral view the frontal carinae do not form a continuous curve with the clypeus (Fig. 17) (in contrast to the *P. subtilissimus* group, see below and Fig. 19); median lobe of clypeus tectiform, notably produced anteriorly, the anterior margin sharp-edged and weakly flared (Figs. 14–16); in dorsal view anterior margin of median clypeal lobe convex and laterally rounded; petiolar node relatively short and high (PLI 0.67–1.06), anterior peduncle not conspicuously developed. Head and mesosoma at least partly punctate, and usually with substantial areas of the integument opaque or subopaque. Erect pilosity conspicuous on most parts of body, including the antennae, legs, head, and dorsum of mesosoma. Body covered with light to moderate density of fine pubescence. Palpal formula: 6,3 (reduced to 5,3 in *P. eduardi, P. pisinnus*, and in some individuals of *P. caeciliae* and *P. urbanus*; these species are among the smallest in the group).

Comments.— The present concept of the *P. oculatus* group is a much expanded one from that given in Kempf (1961), who treated only three species. Within the *P. oculatus* group, I have included also the cluster of species allied to *P. elongatus* (Mayr) (the "*elongatus* group" of Ward [1985]). As presently defined, the *P. oculatus* group is minimally diagnosed by the following combination of worker features: tectiform clypeal lobe, with weakly flared, sharp-edged, anterior margin (Figs. 14–16); relatively short, high, apendunculate petiole (*e.g.*, Figs. 7, 8, 9b, 10b); and conspicuous standing pilosity. Relationships with the *P. subtilissimus* group are discussed under the latter.

Within the *P. oculatus* group are several reasonably distinctive species, but a bewildering residue of forms remains centering around *P. caeciliae* (Forel), *P. cubaensis* (Forel) and *P. urbanus* (F. Smith). Species relationships within what may be called the *urbanus* complex have not been resolved fully in this study, and will require more extensive material and further analysis (particularly larger samples of worker-associated males and queens).

Synonymic List of Species

    P. alustratus Ward, *sp. nov.* Peru
    P. caeciliae (Forel, 1913), *stat. nov.* Texas to Panama
    P. cretus Ward, *sp. nov.* Guatemala, Costa Rica
    P. cubaensis (Forel, 1901b). Caribbean; Mexico to Bolivia
    P. curacaensis (Forel, 1912). Panama to Bolivia, Brazil
    P. eduardi (Forel, 1912). Jamaica; Costa Rica to Peru, Brazil
    P. elongatus (Mayr, 1870). Florida; Mexico to Bolivia, Brazil
        = *P. alliodorae* (Wheeler, 1942), *syn. nov.*
        = *P. allidorus* (Enzmann, 1945).
        = *P. tandem* (Forel, 1906).
    P. oculatus (F. Smith, 1855). Mexico to Bolivia, Brazil
        = *P. advena* (F. Smith, 1855).
        = *P. dolichopsis* (Forel, 1899).
        = *P. implicatus* (Forel, 1911).
        = *P. altinodus* (Mann, 1916), *syn. nov.*
        = *P. tuberculatus* (Enzmann, 1945), *syn. nov.*
        = *P. wessoni* (Enzmann, 1945), *syn. nov.*
    P. pisinnus Ward, *sp. nov.* Brazil, Peru
    P. schuppi (Forel, 1901a). Argentina, Paraguay, Brazil
        = *P. confusior* (Forel, 1901a).
        = *P. geraensis* (Forel, 1912).
    P. urbanus (F. Smith, 1877). Panama, South America
        = *P. chodati* (Forel, 1920), *syn. nov.*
        = *P. ogloblini* (Santschi, 1936), *syn. nov.*

Key to Species (workers and queens)

Note.— The queen caste is included tentatively in this key. To underscore the rather limited amount of material on which this is based, I have given sample sizes (n = ...) for queen measurements. Sample sizes within single lugs of a couplet are all identical, and are not repeated after the first metric measurement.

1   Petiolar node broadly rounded in lateral profile, without strongly differentiated dorsal and posterior faces (*e.g.,* Figs. 8,9b); summit of the node usually occurring in the middle third of the petiole length (NI 0.51–0.69) 2

1'   Petiolar node with a flat, posteriorly uplifted, dorsal face, rounding suddenly into a vertical posterior face (Fig. 7); summit of node displaced to the posterior quarter of the petiole length (NI 0.72–0.85); medium-sized species (worker HW 0.73–0.91; queen HW 0.78–0.85, n=7) with broad head (worker CI 0.77–0.87; queen CI 0.71–0.76) and long eyes (worker REL 0.55–0.62; queen REL 0.53–0.57) (Mexico to Bolivia and Brazil) ....*P. oculatus* (F. Smith), p. 422

2   (1)   Larger species, worker HW 0.74–0.98, usually greater than 0.79 (queen HW 0.78–0.95, n=15); if HW <0.79mm, then occipital margin of head concave (in frontal view) and dorsolateral margination of petiole relatively sharp so that in dorsal view the maximum petiole width appears to coincide with the lateral margination; funicular segments II and III ranging from   slightly broader   than long to   notably longer than broad 3

2'   Smaller species, HW <0.79; occipital margin of worker flat to weakly concave (in frontal view); dorsolateral margination of petiole rather gentle so that in dorsal view the maximum petiole width occurs slightly below the margination; funicular segments II and III broader than long, usually markedly so............... 5

3   (2)   Petiole about as high as long in worker (Fig. 8) (worker PLI 0.94–1.07) and appearing about as broad as long in dorsal view (PWI 0.84–0.99) (in queens: PLI 0.81–0.85, PWI 0.78–0.85, n=4); head densely punctate, opaque (Argentina, Paraguay, s.e. Brazil) .... *P. schuppi* (Forel), p. 426

3'   Petiole longer than high (Figs. 9b,10b) (worker PLI 0.71–0.89; queen PLI 0.57–0.76, n=11) and notably longer than broad in dorsal view (worker PWI 0.59–0.78; queen PWI 0.61–0.75); head punctate and sublucid, with small shiny interspaces between many of the punctures 4

4   (3')   Larger species (worker HW 0.85–0.98; queen HW 0.90–0.95,

n=3) with longer scapes and shorter eyes (worker SI2 0.74–0.80; queen SI2 0.69–0.73; worker REL2 0.62–0.65; queen REL2 0.68–0.71) (Fig. 9a); regressions of HL on HW and EL on HW lying below those of *curacaensis* (Figs. 26, 27) (Guatemala, Costa Rica)......................*P. cretus, sp. nov.*, p. 412

4' Smaller species (worker HW 0.74–0.89; queen HW 0.78–0.88, n=8) with shorter scapes and relatively longer eyes (worker SI2 0.60–0.74; queen SI2 0.58–0.66; worker REL2 0.64–0.77; queen REL2 0.72–0.82) (Fig. 10a); regressions of HL and EL on HW lying above those of *cretus* (Figs. 26,27) (Panama south to Bolivia and Brazil)....................*P. curacaensis* (Forel), p. 416

5 (2') Punctures on dorsum of worker head and pronotum contiguous almost throughout, rendering the integument largely opaque; in particular, punctures mostly contiguous and without extensive shiny interspaces (*i.e.,* separated by half their diameters or less) posteromesad of compound eye, and immediately posterior to compound eye (except for a thin shiny margin about 0.010–0.020 mm. wide), when viewed under a light microscope (see also SEM micrographs, Figs. 20, 21); queens similar but sometimes with slightly more extensive shiny interspaces between ocelli and compound eye.. 6

5' Dorsum of head and pronotum more extensively shiny or sublucid, especially in queens; at least some punctures separated by half their diameters or more, especially between the ocelli and compound eye, and immediately posterior to compound eye, when viewed under a light microscope (see also SEM micrographs, Figs. 22–25)... 7

6 (5) Smaller species (worker HW 0.56–0.68, usually <0.65; queen HW 0.56–0.61, n=19; worker HL 0.73–0.93; queen HL 0.87–0.97) (Florida; Mexico south to Bolivia and Brazil) ....
....*P. elongatus* (Mayr), p. 419

6' Larger species (worker HW 0.69–0.75; queen HW = 0.67, n=1; worker HL 0.96–1.04; queen HL = 1.05) (Peru) ....
....*P. alustratus, sp. nov.*, p. 409

7 (5') Very small species (worker HW 0.47–0.51, queen unknown); worker with elongate head (CI 0.61–0.68), short scapes (SI2 0.50–0.54), long basal face of propodeum (PDI 1.46–1.69), and low petiole (PLI 0.67–0.77) (Fig. 11); light orange-brown (Brazil, Peru)..................................... *P. pisinnus, sp. nov.*, p. 425

7' Larger species (worker HW 0.50–0.78) with broader head (worker CI 0.67–0.79) and longer scapes (worker SI2 0.55–0.74); at lower end of worker size range (HW 0.50–0.60),

basal face of propodeum shorter (PDI 0.91–1.45) and petiole higher (PLI 0.79–0.92); color variable, often medium to dark brown 8

8 (7') Front of head smooth and shiny with scattered fine punctulae (Fig. 25); small (worker HW 0.50–0.57; queen HW 0.51–0.55, n=3), dark brown, shiny species (Jamaica; Costa Rica to Peru and Brazil) .... *P. eduardi* (Forel), p. 418

8' Front of head shiny to subopaque, with coarser (0.010 to 0.020 mm in diameter) and denser punctures, separated by 0–4 diameters (*e.g.*, Fig. 24); size and color variable (*urbanus* complex) 9

9 (8') Larger species (worker HW 0.65–0.78; queen HW 0.65–0.76, n=17); at lower end of worker size range, fore femur is relatively slender and eyes relatively short (see Figs. 28,29) (Florida, West Indies, Mexico south to Brazil) .... *P. cubaensis* (Forel) (*s.l.*), p. 413

9' Smaller species (worker HW 0.51–0.66; queen HW 0.51–0.64, n=9); at upper end of worker size range, fore femur tends to be broader and eyes longer (Figs. 28,29) 10

10 (9') Larger species (worker HW 0.58–0.66; queen HW 0.58–0.64, n=3); ocellar distance (OD) generally smaller (worker OD/HW 0.103–0.149) (see Fig. 30); usually light orange-brown in color, sometimes darker (Panama, South America)................................ .... *P. urbanus* (F. Smith), p. 427

10' Smaller species (HW 0.51–0.61, usually < 0.59; queen HW 0.51–0.59, n=6), with a larger ocellar distance (worker OD/HW 0.127–0.169) (see Fig. 30); medium to dark brown in color (Texas south to Panama)................... *P. caeciliae* (Forel), p. 410

Species Accounts

Pseudomyrmex alustratus sp. nov.
(Figures 13a, 13b)

Holotype worker.— PERU, Junín: Chanchamayo, Anashirone River, 16.vii.1963, C.A. Portocarrero #A47 (Kempf No. 4060) (MZSP). HW 0.73, HL 1.03, EL 0.59, PL 0.42, PH 0.35.

Paratypes.— Five workers, same data as holotype (BMNH, LACM, MCZC, MZSP). Seven workers, one dealate queen, same locality as holotype, 22.viii.1963, C.A. Portocarrero #73 (Kempf No. 4072) (MJPL, MZSP, PSWC).

Additional non-paratypic material is listed below.

Worker measurements (n=9).— HL 0.96–1.04, HW 0.69–0.75, MFC 0.018–0.024, CI 0.70–0.76, OI 0.55–0.58, REL 0.55–0.58, REL2 0.76–0.80, OOI 0.13–0.53, VI 0.80–0.86, FCI 0.024–0.034, SI 0.45–0.46, SI2 0.58–0.60, FI 0.47–0.53, PDI 1.32–1 58, MPI 0.040–0.055, NI 0.59–0.64, PLI 0.83–0.92, PWI 0.63–0.71, PPWI 1.18–1.43.

Worker diagnosis.— Medium-sized species (HW 0.69–0.75), with elongate head and eyes (Fig. 13a; CI 0.70–0.76, REL2 0.76–0.80); sides of head slightly convex, occipital margin weakly concave in full-face view; second and third funicular segments broader than long (FLI 1.49–1.69, n=5). Fore femur relatively broad; metanotal groove of moderate depth but not long; basal face of propodeum flat to slightly convex, not notably raised above level of mesonotum, longer than the declivitous face into which it rounds rather suddenly (the basal and declivitous faces of the propodeum form a distinct obtuse angle in some individuals). Petiolar node relatively short and high (Fig. 13b; see metrics), with a conspicuous, rounded subpetiolar process; postpetiole broader than long.

Mandibles striate with scattered punctures. Head and pronotum densely punctate and opaque (weakly sublucid in the centre of the pronotum); remainder of mesosoma punctate or coriarious-imbricate, and subopaque. Petiole, postpetiole, and gaster subopaque to weakly shining, with numerous fine piligerous punctures. Fine erect pilosity and appressed pubescence common over most of the body, including the mesosoma dorsum. Medium brown, apices of appendages (antennae, legs) lighter in color; mandibles pale luteous.

Comments.— This species evidently is related closely to *P. elongatus*, from which it differs primarily in size (HW >0.68). The head is even more densely punctate and opaque than in most *P. elongatus* workers, the basal face of the propodeum tends to be relatively longer (compare PDI values), and the subpetiolar process is perhaps a little better developed than in *P. elongatus*. The punctate opaque head, elongate eyes (REL2 >0.76), relatively broad fore femur, and high, rounded petiole (PLI >0.82), distinguish *P. alustratus* from *P. cubaensis*, the only species with which it overlaps substantially in size.

Biology.— Essentially nothing is known about the biology of *P. alustratus*. Two workers from Sotileja, Peru were foraging on *Ochroma*.

Material Examined.— Type material listed above plus the following: PERU Junín: Valle Chanchamayo, 800m (Weyrauch) (MZSP); *Madre de Dios*: Sotileja, jct. Rio Manu & R. Sotileja (D.W. Davidson) (PSWC).

<center>

Pseudomyrmex caeciliae (Forel), *stat. nov.*
(Figures 23, 24, 28, 29, 30)

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Pseudomyrma eduardi race *caeciliae* Forel, 1913: 214. Two syntype workers, Patulul, Guatemala (Peper) (MHNG) [Examined]. One worker here designated LECTOTYPE.

Worker measurements (n=26).— HL 0.73–0.91, HW 0.51–0.61, MFC 0.012–0.023, CI 0.67–0.74, OI 0.52–0.60, REL 0.48–0.55, REL2 0.72–0.81, OOI 0.22–0.80, VI 0.73–0.91, FCI 0.021–0.041, SI 0.42–0.49, SI2 0.55–0.63, FI 0.45–0.51, PDI 0.91–1.45, MPI 0.048–0.084, NI 0.55–0.63, PLI 0.79–0.91, PWI 0.61–0.74, PPWI 1.09–1.39.

Worker diagnosis.— Small species (HW 0.51–0.61) with elongate eyes (REL2 0.72–0.81); ocelli relatively well-separated, OD/HW > 0.127; sides of head subparallel, rounding into the occipital margin, the latter flat to weakly concave, in full-face view; second and third funicular segments broader than long, usually notably so (FLI 1.23–1.72, n=5). Fore femur relatively broad; metanotal groove well marked; basal face of propodeum flat to weakly convex, often raised perceptibly above the level of the mesonotum; basal face rounding into declivitous face of propodeum, to which it is subequal or slightly greater in length (see PDI values). Petiole relatively short and high (PLI >0.79), with an anteroventral process, variously developed; postpetiole of typical dimensions, broader than long.

Mandibles striate (sometimes weakly so), with scattered punctures. Head densely punctate, the punctures separated by shiny interspaces at least on parts of the upper third of the head, and especially in the area immediately posterior to the compound eye, so that these parts of the head appear sublucid to shiny (in contrast to the predominantly opaque head of *P. elongatus*); head punctures (Figs. 23, 24) relatively coarse, 0.010 to 0.020 mm in diameter; mesosoma punctate to coriarious-imbricate, sublucid in the centre of the pronotal and mesonotal discs, and on the side of the pronotum, more opaque elsewhere; petiole, postpetiole, and gaster sublucid, with numerous fine piligerous punctures. Fine, erect pilosity (sometimes rather short) and appressed pubescence common over most of the body, including the mesosoma dorsum. Body medium to dark brown in color, the mandibles, antennae, and tarsi varying from concolorous to a paler luteous brown.

Comments.— This previously overlooked species ranges from Texas to Panama. It includes populations from Texas and parts of Mexico which I misidentified as *P. elongatus* in Ward (1985). The characteristic features of *P. caeciliae* are its small size, relatively dark color, and the sublucid punctate appearance of parts of the head and mesosoma. It is distinguished from *P. elongatus* primarily on the basis of this shiny appearance (all of their metric measurements overlap broadly, although *P. elongatus* averages larger in size, with relatively longer eyes – compare HW, HL and REL). Typically *P. elongatus* workers have a densely punctate and opaque head, while in *P. caeciliae* the punctures on the head are less dense, with (correspondingly) more extensive shiny interspaces between them, especially in the area immediately posterior to the compound eye (see Figs. 20, 21, 23); but both species vary considerably, and the extremes of sculptural variation come close to overlapping.

Among material examined in the present study, an old series of workers from Escuintla, Guatemala (Wheeler leg.) included both *P. elongatus*, *P. caeciliae*, and several individuals seemingly intermediate between the two. In western Mexico (Jalisco, Sinaloa), where *P. caeciliae* is apparently absent, some *P. elongatus* workers approach *P. caeciliae* in head sculpture. On the other hand in Costa Rica, where the two species are broadly sympatric, I have seen no intermediates among material referable to the two species.

P. caeciliae differs from *P. cubaensis* by its smaller size (HW <0.62), relatively longer eyes (REL2 0.72–0.81) (Fig. 28), broader fore femur (Fig. 29), and shorter petiole. While Mexican and Central American populations of these two species are rather distinct, Jamaican "*caeciliae*" partly bridge the gap between the two. These Jamaican individuals may, in fact, represent small *P. cubaensis*.

The relationship of *P. caeciliae* to the South American species, *P. urbanus*, is even more problematic. The existing differences between the two are slight (see key to species) and not wholly diagnostic. More material, especially worker-associated queens and males from northern South America, will be needed to resolve this issue.

Biology.— *P. caeciliae* has been collected nesting in dead twigs of *Quercus* and *Prosopis* in Texas and northern Mexico. Costa Rican nest-site records include dead twigs of *Gliricidia sepium, Anacardium* and *Laguncularia racemosa*. Habitat records cover a broad range (tropical dry forest, mangrove, littoral vegetation, riparian forest, edge of second-growth rain forest, rain forest) but suggest a

preference for open areas. In Costa Rica the species is notably less common than *P. elongatus*.

Material Examined (CDAE, CNCC, GCWC, JTLC, LACM, MCZC, MHNG, MZSP, PSWC, USNM).—

COSTA RICA *Guanacaste*: 6 mi S, 6 mi W Cañas, Taboga (D. H. Janzen); Hda. La Pacifica, nr. Cañas, 50 m (P. S. Ward); Palo Verde (C. M. Herrera); Santa Rosa Natl. Pk. (D. H. Janzen); Santa Rosa Natl. Pk., < 5 m (P. S. Ward); *Limon*: Talia Farm, Estrella Valley (G. C. Wheeler); *Puntarenas*: 9.7 mi W Esparta (D. H. Janzen); Boca Barranca (D. H. Janzen); Estrella, 300 m (J. T. Longino); Golfito, 5 m (P. S. Ward); Manuel Antonio Natl. Pk., 10 m (P. S. Ward); Manuel Antonio Natl. Pk., < 5 m (P. S. Ward); Pita, 120 m (J. T. Longino); Pita, 200 m (J. T. Longino); Sarmiento, 200–300 m (J. T. Longino); Sirena, Corcovado Natl. Pk., 10 m (P. S. Ward); Sirena, Corcovado Natl. Pk., 50 m (J. T. Longino); *San José*: 2 mi. W Río Oro (D. H. Janzen); 40 km S San Isidro de General (D. H. Janzen); San José (H. Schmidt).

GUATEMALA *Escuintla*: Escuintla (W. M. Wheeler; N. L. H. Krauss); *Izabal*: Los Amates (Kellerman); *Suchitepéquez*: Patulul (Peper).

HONDURAS *Atlántida*: La Ceiba (F. S. Dyer); *Cortés*: Choloma (W. M. Mann).

JAMAICA Kingston (A. Forel); Ford 1 mi SE Stony Creek (E. A. Chapin).

MEXICO "Mexico", intercepted at Brownsville (c.u.); *Camp.*: 29 mi E, 12 mi S Campeche (Ruinas Edzna) (D. H. Janzen); *N.L.*: El Pastor, Montemorelos, 2200 ft. (W. S. Creighton); *S.L.P.*: 3 mi N Valles, 300 ft. (W. S. Creighton); *Tamps.*: 6.2 mi S San Fernando on Hwy 101 (D. H. Janzen); Cañon del Abra, 1000 ft. (W. S. Creighton); *Ver.*: Camarón (E. Skwarra).

NICARAGUA *Estelí*: 7.5 mi NW San Isidro, 550 m (D. H. Janzen).

PANAMA *Chiriqui*: "Prov. Chiriqui" (F. M. Gaige); *Panamá*: Trinidad Rio (A. Busck).

UNITED STATES *Texas*: *Cameron Co.*: 10 mi W Boca Chica (R. R. Snelling); 5 mi W Boca Chica (G. C. & J. Wheeler); Brownsville (H. S. Barber; c.u.); Harlingen (W. F. Buren); *Hidalgo Co.*: Mission (W. F. Buren); Monte Alto, 60 ft. (W. S. Creighton); *Kenedy Co.*: 26 mi N Raymondsville (W. S. Creighton).

Pseudomyrmex cretus, sp. nov.
(Figures 9a, 9b, 26, 27)

Holotype worker.— COSTA RICA, *Prov. Guanacaste*: Santa Rosa Natl. Park, 300m, 10°51'N, 85°37'W, 14.xii.1983, ex dead twig of *Schoepfia*, tropical dry forest, P. S. Ward acc. no. 6434 (MCZC). HW 0.95, HL 1.18, EL 0.61, PL 0.52, PH 0.42.

Paratypes.— Same locality and date as holotype, P. S. Ward acc. nos. 6434 and 6427–2: two series of workers; COSTA RICA, *Prov. Guanacaste*: Santa Rosa Natl. Park, 270m, 10°50'N, 85°38'W, 14.xii.1983, P. S. Ward acc. nos. 6443, 6444, 6446, and 6448, workers and dealate queens. (BMNH, INPA, IZAV, LACM, MCZC, MJPL, MNCR, MZSP, PSWC, UCDC, UNCB, USNM)

Type material restricted to the above series from Santa Rosa National Park, Costa Rica. Additional material, believed to be conspecific, is listed below.

Worker Measurements (n=14).— HL 0.99–1.22, HW 0.85–0.98, MFC 0.027–0.035, CI 0.78–0.86, OI 0.57–0.60, REL 0.49–0.53, REL2 0.62–0.65, OOI 0.07–0.35, VI 0.74–0.81, FCI 0.028–0.039, SI 0.46–0.50, SI2 0.73–0.80, FI 0.40–0.46, PDI 1.21–1.43, MPI 0.047–0.068, NI 0.60–0.65, PLI 0.77–0.89, PWI 0.69–0.78, PPWI 1.21–1.50.

Worker Diagnosis.— A relatively large species for the *P. oculatus* group (HW 0.85–0.98), with broad head, long scapes, and relatively short eyes (Fig. 9a; SI2 0.73–0.80); sides of head broadly convex, occipital margin weakly concave in frontal view; second and third funicular segments as long as, or longer than, wide (FLI 1.94–2.40, n=5). Fore femur relatively slender; metanotal groove conspicuous but not sharply excavated; basal face of propodeum flat to weakly convex, raised slightly above the level of the mesonotum, longer than the declivitous face from which it is usually well differentiated; juncture of basal

and declivitous faces of propodeum often marked laterally by a slight angle, which continues as weak margination flanking the flat declivitous face. Petiole (Fig. 9b) apendunculate with a well-developed anteroventral process, the node high and broadly rounded in lateral view, rather broad in dorsal view (see petiolar indices); lateral margination of petiolar node more marked than in most other species of the *oculatus* group; postpetiole notably broader than long.

Mandibles striato-punctate; head densely punctate, subopaque, upper third becoming sublucid due to shiny interspaces between the punctures (which are separated by 0.25 to 1.0 their diameters); mesosoma punctate to coriarious-imbricate, the mesonotum and centre and sides of pronotum sublucid, remainder mostly opaque. Petiole, postpetiole, and gaster sublucid, the lustre subdued by numerous fine piligerous punctures and associated pubescence. Fine erect pilosity and appressed pubescence common on most of the body, including mesosoma dorsum; the pilosity a little longer and denser than is typical for the *oculatus* group. Light to medium castaneous brown, the gaster and femora darker brown (variably so), with varying degrees of modest infuscation of the mesosoma; mandibles paler, luteous brown.

Comments.— The combination of large size (HW > 0.84) and petiole shape (node longer than high, broadly rounded in lateral view) separates *P. cretus* from all other species except *P. curacaensis*. *P. cretus* and *P. curacaensis* appear to be sister species; their males both possess unusually lengthened palpal segments and shortened antennal segments, conditions not known to occur in other members of the *P. oculatus* group

The worker of *P. cretus* averages larger in size than that of *P. curacaensis*, and in the region of size overlap (HW 0.85–0.90) it possesses a broader head, shorter eyes, and longer scapes (see Figs. 26, 27, and worker key). The two species have not been collected sympatrically, *P. cretus* being known from Guatemala and Costa Rica, *P. curacaensis* from Panama and most of South America. It is possible that intermediate populations will be located in Central America, and the name *P. cretus* would then become a junior subjective synonym of *P. curacaensis*, but the Panama collections of *P. curacaensis* which I have examined do not approach *P. cretus* in size or head shape.

Biology.— The available records suggest that *P. cretus* is an inhabitant of tropical dry forest. Colonies have been collected in dead twigs of *Gliricidia sepium* and *Schoepfia* sp. at the type locality (Santa Rosa National Park, Costa Rica). At the same locality workers were observed foraging on low vegetation and visiting extrafloral nectaries of *Croton*. Workers collected at Estrella, Costa Rica (J. Longino leg.) appeared to be nesting in a dead fence post.

Material Examined.— Type material listed above, plus the following (JTLC, LACM, MZSP, PSWC):

COSTA RICA *Guanacaste*: 5 km S. Liberia (D. H. Janzen); La Cruz, 250 m (J.T. Longino); Palo Verde (D. E. Gill; C. M. Herrera); Santa Rosa Natl. Park (L. Gillespie; D. H. Janzen); Santa Rosa Natl. Park, 100 m (J. T. Longino); *Puntarenas*: Estrella, 300m (J. T. Longino); Pita, 200m (J. T. Longino).

GUATEMALA *Retalhuleu*: N edge Champerico (D. H. Janzen); 2 mi. NE Champerico (D. H. Janzen).

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Pseudomyrmex cubaensis (Forel)

(Figures 22, 28, 29)

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Pseudomyrma elongata var. *cubaensis* Forel, 1901b: 342. Holotype (unique syntype) worker, Bahia Honda, Cuba (M. J. Schmitt) (MHNG) [Examined].
Pseudomyrma elongata var. *cubaensis* Forel; Forel, 1913: 215. [Description of queen].

Pseudomyrmex elongata; Creighton (nec Mayr), 1955: 18. (partim) [Synonymy of *P. cubaensis* under *P. elongatus*].

Pseudomyrmex cubaensis (Forel); Ward, 1985: 226. [Revalidated as a distinct species].

Worker measurements, Florida and Caribbean (cubaensis s.s.) (n=24).— HL 0.89–1.02, HW 0.65–0.73, MFC 0.017–0.029, CI 0.71–0.75, OI 0.52–0.58, REL 0.47–0.51, REL2 0.65–0.71, OOI 0.41–0.95, VI 0.74–0.84, FCI 0.024–0.044, SI 0.44–0.48, SI2 0.64–0.74, FI 0.42–0.48, PDI 1.09–1.44, MPI 0.038–0.084, NI 0.53–0.63, PLI 0.67–0.78, PWI 0.55–0.71, PPWI 1.01–1.28.

Worker measurements, mainland Latin America (n=31).— HL 0.82–1.06, HW 0.65–0.78, MFC 0.015–0.031, CI 0.69–0.79, OI 0.53–0.60, REL 0.50–0.56, REL2 0.66–0.76, OOI 0.16–0.73, VI 0.75–0.86, FCI 0.022–0.044, SI 0.44–0.50, SI2 0.60–0.72, FI 0.41–0.50, PDI 1.12–1.51, MPI 0.038–0.066, NI 0.54–0.68, PLI 0.75–0.88, PWI 0.57–0.71, PPWI 1.13–1.36.

Worker diagnosis (cubaensis s.s.).— Medium-sized species (HW 0.65–0.73), with elongate head and relatively short eyes (REL 0.47–0.51); sides of head shallowly convex, occipital margin flat to slightly concave, in frontal view; funicular segments II and III broader than long. Fore femur only moderately swollen; metanotal groove conspicuously impressed; basal face of propodeum more or less flat, raised slightly or not at all above level of mesonotum, rounding gently into the declivitous face which it exceeds in length. Petiole apenduculate, with a conspicuous anteroventral process (blunt or tooth-like), node rather long relative to its height (see metrics), and with gentle dorsolateral margination; postpetiole slightly longer than broad.

Mandibles striato-punctate; head (Fig. 22) densely punctate, subopaque to sublucid, with rather conspicuous shiny interspaces between the punctures on the upper third of the head, especially between the ocelli and the compound eye and immediately posterior to the eye. Mesosoma punctate to coriarious-imbricate, subopaque, with sublucid areas on the side of the pronotum and centre of the pronotum and mesonotum; petiolar node sublucid, especially its posterior face; postpetiole and gaster sublucid, covered with numerous fine piligerous punctures. Fine erect pilosity and appressed pubescence covering most of body, including mesosoma dorsum. Medium to dark brown, the antennae, mandibles, and tarsi lighter in color.

Comments.— The above description applies to the populations of *P. cubaensis* inhabiting Florida and the Caribbean. Elsewhere, in Mexico, Central America, and South America is a variable array of *cubaensis*-like populations which I currently treat as conspecific with the Caribbean form. Workers in these mainland populations tend to have longer eyes and a shorter and higher petiole (compare REL, REL2, and PLI in the lists of measurements given above). They also tend to be lighter in color, especially in South America where some populations contain rather large orange-brown workers, quite different in appearance from Caribbean *P. cubaensis*. Taken together as a whole, however, these mainland populations overlap in size, shape, and color with the more typical *P. cubaensis*, and I find no clear discontinuities in the available (largely worker-based) material. Future work involving the analysis of queens, males, or biochemical characters might well reveal several cryptic species.

P. cubaensis (s.l.) can be diagnosed minimally by the combination of medium size (HW 0.65–0.78); a punctate-sublucid head; relatively short eyes (REL2 0.65–0.76); moderately broad fore femur (FI 0.41–0.50); and petiole with rounded dorsolateral margination. The largest workers of *P. cubaensis (s.l.)* from South America overlap in size with the smallest workers of *P. curacaensis*; they are distinguished from the latter by the possession of a broader fore femur, longer head, flatter occipital margin, shorter funicular segments, and gentler dorsolateral margination of the petiole (see discussion under *P. curacaensis*). At the lower limits

of its size range, *P. cubaensis* (*s.l.*) can be difficult to distinguish from *P. urbanus*. Workers of the latter have broader fore femora and longer eyes for a given head width, compared to *P. cubaensis* (*s.l.*) (see scatter plots in Figs. 28 and 29, but note the variation).

Workers of *P. cubaensis* (*s.l.*) differ from those of *P. elongatus* by their larger average size, shorter eyes and lower petiole height in the region of size overlap, and sublucid head and mesosoma.

Biology.— In the Caribbean region, colonies of *P. cubaensis* occupy dead stems of various woody and herbaceous plants (Ward, 1985), often in littoral environments. Mainland populations come from a variety of habitats, including tropical dry forest, savannah, roadside verge, second-growth lowland rain forest, rain forest edge and montane rain forest edge. Nesting habits of these mainland populations are probably also generalized, but unfortunately most records consist of foraging workers rather than nest series.

Material examined (BMNH, CASC, CKIC, CNCC, CUIC, EBCC, INPA, IZAV, JTLC, KWJC, LACM, MCSN, MCZC, MHNG, MNHN, MZSP, PSWC, UCDC, USNM, WPMC).—

P. cubaensis (*s.s.*)

BAHAMAS Andros I. (W. M. Wheeler); Conception I., S. Bahamas (J. Greenway); Crooked Is., Gun Point (B. Valentine & R. Hamilton); Fish Hawk Key, Andros I. (W. M. Wheeler); High Ridge Cay (W. M. Mann); Mangrove Cay, Andros I. (B. Cole); Nassau (W. M. Wheeler); New Providence (B. Cole).

CAYMAN ISLANDS. Grand Cayman (M. E. C. Giglioli); Little Cayman (F. Banks).

CUBA "Cuba" (Cresson; c.u.); 7 km N Vinales (c.u.); Aguada de Pasajeros (W. M. Wheeler); Anafe, Habana (G. Aguayo); Bahia Honda (Wickham; c.u.); Bolondron (W. M.Wheeler); Cabada (W. M. Mann); Cabanas, Pinar del Rio (c.u.); Cayamas (Baker; E. A. Schwarz); Cienaga de Zapata (W. M. Wheeler); Cienfuegos (W. M. Mann); Cristo (W. M. Mann); El Caney (W. M. Mann); Gomez Mena (San Nicholas) (G. Salt); Guanajay, Pinar del Rio (E. O. Wilson); Guantanamo (W. M. Mann); Guavivo Cave, Soledad (Fal. Smith); Hanabanilla Falls, Trinidad Mts. (G. Salt); Harvard Bot. Gardens, Soledad, Cienfugos (N. A. Weber); Havana (A. Bierig; P. Serre); Hormiguero (H. J. MacGillavry); Jaruca, Habana (P. Bermudez); Jiquari (Barbour & Shaw); Juraguà, Las Villas Prov. (E. O. Wilson); La Milpa, nr. Cienfugos (G. Salt); Limones (W. M. Mann); Limones Seboruco (N. A. Weber); Malas Aguas, Pinar del Rio (E. O. Wilson); Mina Carlota, Trinidad Mts. (W. M. Mann); Pied. de las Tunas (W. M. Mann); Pinar del Rio (H. J. MacGillavry); Pinares, Oriente (W. M. Mann); Rio Hanabana (c.u.); San Blas, Trinidad Mts., Santa Clara (c.u.); Santa Clara, Las Villas Prov. (E. O. Wilson); Soledad (J. G. Myers; Fal. Smith); Soledad Gardens (F. M. Carpenter); Soledad, Cienfuegos (C. T. Brues; C. T. & B. B. Brues; W. S. Creighton; Darlington); Soledad, nr. Cienfuegos (N. Banks); Viñales, Pinar del Rio (A. F. Arden); nr. Casa Harvard, Soledad, Cienfuegos (N. A. Weber).

HAITI "Haiti" (E. C. Leonard); Grande Rivière (W. M. Mann); Mts. N of Jacmel (W. M. Mann).

JAMAICA Balaclava (Wight); Bluefields Bay (E. A. Chapin); Kingston (N. L. H. Krauss; c.u.); St. Eliz., Pedro Cross, 230 m (J. T. Longino); Troy (Wight); Westmor, Auchindown, 150 m (J. T. Longino).

UNITED STATES *Florida: Charlotte Co.*: 5 mi S Punta Gorda (E. S. Ross); Punta Gorda (c.u.); *Collier Co.*: Collier-Seminole St. Pk. (P. S. Ward); Marco (W. T. Davis); *Dade Co.*: no specific locality (J. N. Knull); Biscayne Bay (A. Slosson); Cards Point (W. M. Wheeler); Long Pine Key (W. M. Wheeler); Miami (F. N. Young); Miami & vicinity (A. E. Wight); Miami Beach (W. L. Brown; A. C. Cole); Paradise Key (D. Fairchild; A. Wetmore; W. M. Wheeler); Paradise Key, Everglades Nat. Pk. (T. H. & S. P. Hubbell); *Highlands Co.*: no specific locality (F. J. Moore); Archbold Biol. Stn. (R. Silberglied); Highlands Hammock St. Pk. (L. & C. W. Obrien); nr. Sebring (R. W. Klein); *Hillsborough Co.*: no specific locality (J. C. Bowyer; R. F. Tinker); Tampa (M. H. Muma); *Lake Co.*: no specific locality (W. A. Hiers); *Lee Co.*: "Ft. Meyers" (c.u.); Ft. Myers (J. C. Bradley); *Monroe Co.*: Key West (c.u.); Lower Matecumbe Key (W. M. Wheeler); N. Key Largo (R. W. Klein); No Name Key (P. S. Ward); *Osceola Co.*: Lake Alfred (M. H. Muma); *Palm*

Beach Co.: Boynton Beach (Wood & Davidson); *Sarasota Co.*:30mi SE Sarasota, T38S, R22E, S.33 (J. T. Longino); Long Branch Key, Sarasota (A. C. Cole); Sarasota (A. C. Cole); *Seminole Co.*: Sanford (A. B. Gahan).

P. cubaensis, mainland

ARGENTINA *Misiones*: El Dorado (N. Kusnezov); Esperanza (N. Kusnezov); *Salta*: Coronel Moldes (Monros).

BOLIVIA *Beni*: 14 km SW San Borja, 210 m (P. S. Ward); Espiritu (F. Koya).

BRAZIL *AM*: Ig. Marianil, Rio Branco Rd., 24 km NE Manaus (W. L. Brown); Manaus to Itacoatiara Hwy, km. 34 (W. L. & D. E. Brown); *MT*: Vila Vera (M. Alvarenga); *PA*: C. Araguaía (J. A. Rafael); Tucurui (W. L. Overal); *PE*: Ilha Fernando Noronha (M. Alvarenga); *RJ*: Monumento Rodoviário (c.u.).

COLOMBIA *Cauca*: Popayán (W. & E. MacKay); Medellin, 1800 m (N. A. Weber); *Magdalena*: Gairaca Bay, Parque Tayrona, 0–5 m (C. Kugler); *Meta*: Pto. López (W. & E. MacKay).

COSTA RICA "Costa Rica" (F. Nevermann); *Alajuela*: 11 mi N Florencia (D. H. Janzen); *Guanacaste*: Est. Biol. Palo Verde, 10 m (J. T. Longino); N side Lago de Arenal, 570 m (J. T. Longino); Palo Verde (C. M. Herrera); *Heredia*: 3km S Pto. Viejo, 50 m (J. T. Longino); *Limon*: 5 mi. W Guapiles (D. H. Janzen); Hamburg Farm, Santa Clara (F. Nevermann); *Puntarenas*: 1 km NE Tárcoles, 20 m (P. S. Ward); Monteverde, 1100 m (P. S. Ward); Ojo de Agua, 800 m (J. T. Longino); Sirena, Corcovado Natl. Pk., 0–100 m (J. T. Longino); Sirena, Corcovado Natl. Pk., 50 m (J. T. Longino); *San José*: San Isidro de General (C. L. Hogue); San José (H. Schmidt).

GUATEMALA *Escuintla*: Escuintla (W. M. Wheeler); *Guatemala*: hills above Lake Amatitlán (D. H. Janzen); *Izabal*: Lago Izabal, 1.5 km NE El Estor (D. H. Janzen).

GUYANA *Mazaruni-Potaro*: Kartabo, Bartica Dist. (W. M. Wheeler); Kartabo Point (W. Steiner *et al.*).

MEXICO *Camp.*: 29 mi E, 12 mi S Campeche (Ruinas Edzna) (D. H. Janzen); *Gro.*: 25.4 mi S Chilpancingo (D. H. Janzen); *Is. Tres Marias*: Maria Madre I. (H. H. Keifer); Maria Magdalena I. (R. R. Snelling); *Jal.*: Est. Biología Chamela, 100 m (P. S. Ward); *Mich.*: 9 mi E Capirio, 800 ft. (E. Fisher & P. Sullivan); *Mor.*: 5 mi S Cuernavaca (W. S. Ross); *Sin.*: 20 mi E Villa Union, 235 m (E. I. Schlinger); *Tab.*: 3 mi W Cárdenas (D. H. Janzen); 13 km W border Chiapas, Rt. 186 (W. P. MacKay); *Ver.*: 9 km NNW Sontecomapan, 20 m (P. S. Ward); 10 km NW Isla, Ruta 145, 10 m (W. P. MacKay); Est. Biol. "Los Tuxtlas", nr. San Andres Tuxtlas (G. Ibarra M.); Los Tuxtlas, 10 km NNW Sontecomapan, 200 m (P. S. Ward); Mirador (E. Skwarra); Palma Sola (P. Reyes); Sontecomapan (D. H. Janzen).

PANAMA *Canal Zone*: vic. Pta de los Chivos, 3 km SW Gatun, 100 m (W. L. Brown *et al.*).

PERU *Loreto*: Yurac, 67 mi E Tingo Maria (E. I. Schlinger & E. S. Ross).

VENEZUELA *Aragua*: El Limon, 480 m (C. J. Rosales); *Barinas*: Pueblo Nuevo (H. Romero); 17 km SSW Ciudad Bolivia, 240 m (P. S. Ward); *Cojedes*: 20 km W San Carlos (W. L. & D. E. Brown); *Monagas*: Caripe (EMC, JL, CHFH); Uverito (C. J. Rosales & J. A. Gonzales).

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Pseudomyrmex curacaensis (Forel)

(Figures 10a, 10b, 26, 27)

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Pseudomyrma dolichopsis var. *curacaensis* Forel 1912: 29. Two syntype workers, Curaçao (Bugnion) (MHNG) [Examined]. One syntype here designated LECTOTYPE.

Pseudomyrmex curaçaoensis [sic] (Forel); Kempf, 1961: 379 [Raised to species].

Worker measurements (n=37).— HL 0.85–1.21, HW 0.74–0.89, MFC 0.014–0.037, CI 0.70–0.88, OI 0.53–0.59, REL 0.51–0.58, REL2 0.64–0.77, OOI (–0.04)–0.47, VI 0.74–0.86, FCI 0.018–0.044, SI 0.44–0.49, SI2 0.60–0.74, FI 0.42–0.49, PDI 1.09–1.60, MPI 0.030–0.059, NI 0.56–0.69, PLI 0.71–0.89, PWI 0.59–0.78, PPWI 1.15–1.64.

Worker diagnosis.— Similar to *P. cretus* (*q.v.*); averaging smaller in size (HW 0.74–0.89), with longer head, shorter scapes, and longer eyes (Fig. 10a) (SI2 0.60–0.74; REL2 0.64–0.77) (see also Figs. 26 and 27); occipital margin varying from flat to (frequently) rather conspicuously concave, in full-face frontal view; funicular segments II and III about as long as broad, or nearly so (FLI 1.55–2.04, n=6). Propodeum and petiole (Fig. 10b) similar to that of *P. cretus*, except correspondingly more slender in smaller individuals. Sculpture, pilosity, and pubescence more or less as in *P. cretus*. Color variable: typically medium to dark brown, with lighter appendages, and a darker infuscated patch on the upper third of the

head, including the ocelli; some populations (*e.g.,* northern Colombia, Curaçao) have workers which are lighter orange-brown in color, with contrasting dark brown hind femur, postpetiole, and gaster.

Comments.— It is curious that this species, one of the more common members of the *P. oculatus* group, has been unrecognized since its original description. Kempf (1961) raised *P. curacaensis* to species without being able to identify any material referable to it. In collections I have often found specimens of *P. curacaensis* misidentified as *P. oculatus*, to which they bear only a superficial resemblance, having a very different petiole shape (compare Figs. 7 and 10b) and head sculpture.

The key characteristics of *P. curacaensis* are its relatively large size, sublucid-punctate head, and relatively sharp lateral margination of the petiole (such that, in dorsal view, the maximum width of the petiole occurs at, rather than below, the dorsolateral margination). In lateral view, the petiolar node (Fig. 10b) presents a rounded profile, typical of the *P. oculatus* group. *P. curacaensis* is very closely related to the Central American species, *P. cretus*; for distinguishing features see the description above, the keys to workers and queens, and the discussion under *P. cretus*. At the lower end of its size range (worker HW 0.74–0.79), *P. curacaensis* may be confused with *P. cubaensis* (*s.l.*); the most useful distinguishing characters are the marginate petiole, more markedly concave occipital margin, and the more elongate funicular segments, of *P. curacaensis*. The infuscated patch around the ocelli also tends to be characteristic, but it is not invariably present. Finally, *P. curacaensis* tends to have a less elongate head, and a more slender fore femur, than *P. cubaensis*.

Biology.— I have encountered this species in a broad range of habitats, from tropical thorn forest and roadside vegetation to primary and second-growth rain forest. Nest-site records include dead twigs or branches of *Prosopis juliflora, Gliricidia sepium, Triplaris* sp., *Pilosocereus lanuginosus*, and unidentified bombacaceous and leguminous trees.

Material examined (BMHN, CASC, CDAE, GHPC, INPA, IZAV, KWJC, LACM, MCSN, MCZC, MHNG, MNHN, MZSP, NHMB, PSWC, UCDC, USNM, UWEM, WPMC, WWBC).—

BOLIVIA *Beni*: Blancaflor (W. M. Mann); Espiritu (F. Koya).

BRAZIL *AM*: "Amazonas" (Bates); Praia Grande, Rio Negro, Manaus (W. W. Benson); Res. Campina, Manaus (W. W. Benson); Rio Tarumá Mirim–Igapó (J. Adis); Tarumá-Mirim (J. Adis); *BA*: Salvador (W. W. Kempf); *CE*: Itapipoca (C. R. Gonçalves); *GO*: Jatai (F. M. Oliveira); *MA*: Bacabal (W. W. Kempf); *MG*: Arassuahy (Thieman); Campo Grande (Gilbert & Müller); *MS*: Faz. Dr. José Mendes, Três Lagoas (Exp. Depto. Zool.); *MT*: Barao de Melgaço (W. F. Buren); Pluva, 15 km N I. de Taiamá (C. R. F. Brandão); Sto. Antônio (c.u.); Utiariti, Rio Papagaio, 325 m (K. Lenko); *PA*: Belém (W. F. Buren; C. R. Gonçalves); Cach. Cajú (Sampaio); Igarapé-Açu (c.u.); Soure (c.u.); *PE*: Olinda (Reichensperger); *RD*: Porto Velho (C. R. Gonçalves); *RN*: Ceará-Mirim (W. M. Mann); *RR*: Boa Vista (C. R. Gonçalves); *SP*: Faz. Itaquerê, Bôa Esperança do Sul (K. Lenko); Faz. Itaquerê, Nova Europa (K. Lenko).

COLOMBIA *Guajira*: Maicao (W. L. Brown & C. Kugler); Serrania de Macuira, 6–8 km S Nazareth (W. L. Brown & C. Kugler); *Huila*: 10 km. SE Hobo (W. & E. MacKay); 12 km. S Neiva (W. & E. MacKay); 8 km. S Neiva (W. & E. MacKay); Colombia (W. & E. MacKay); *Magdalena*: 5 km SE Rio Frio, 100 m (P. S. Ward); Arroyo de Arena (F. M. Gaige); Gairaca, Parque Tayrona (C. Kugler); Rio Frio (Darlington); Rio Frio, 20 m (P. S. Ward); Santa Marta, 40 m (P. S. Ward); *Meta*: Carimagua, 370 m (M. Corn); El Castillo (W. & E. MacKay); *Tolima*: Ibagué (W. & E. MacKay).

CURAÇAO "Curacao" (Bugnion); Damacar (J. Maldonado C.).

ECUADOR *prov. unknown*: Limon Cocha & vic. (H. R. Hermann).

FRENCH GUIANA Cayenne (Pillault); Roura (G. H. Perrault).

GUADELOUPE no locality specified (A. Bonfils).

GUYANA *Mazaruni-Potaro*: Forest Settlement, R. Mazaruni (N. A. Weber); Kartabo, Bartica Dist. (W. M. Wheeler); *Rupununi*: Dadanawa, 100 m (J. T. Longino); Karanambo, 100 m (J. T. Longino).

PANAMA *Canal Zone*: 5 km WNW Gatun Dam, 160 m (P. S. Ward); Frijoles (W. M. Wheeler); vic. Pta de los Chivos, 3 km SW Gatun, 100 m (W. L. Brown *et al.*); *Coclé*: La Negrita, nr. Penonomé (D. Cordero); *Colón*: Colón (E. Adams); *Panamá*: Las Cumbres (M. Daykin); Matías Hernández (N. L. H. Krauss); Rio Piedras (D. H. Janzen).

PERU *Huánuco*: Monson Valley, Tingo Maria (E. I. Schlinger & E. S. Ross); Panguana, 220 m (M. Verhaagh); *Madre de Dios*: 30 km SW Pto. Maldonado, 290 m (T. L. Erwin *et al.*); *San Martín*:: 24 km NNE Tarapoto, 220 m (P. S. Ward); Convento, 26 km NNE Tarapoto, 220 m (P. S. Ward); La Perla, 21 km NNE Tarapoto, 220 m (P. S. Ward); Tarapoto, 350 m (P. S. Ward).

ST. VINCENT Layou, St. Vincent (J. F. Lynch); Leeward side, St. Vincent (H. H. Smith); St. Vincent (c.u.).

TRINIDAD "Trinidad" (A. Forel; N. A. Weber; c.u.); Curepe (F. D. Bennett); Imp. Coll. Trop. Agr. (R. D. Shenefelt); Mayaro Bay (N. A. Weber); Nariva Swamp (N. A. Weber); St. Augustine (N. A. Weber).

VENEZUELA *Anzoátegui*: La Leona (H. Romero); *Aragua*: El Limon, 450 m (C. J. Rosales); Maracay, 450 m (P. S. Ward); *Barinas*: 17 km SSW Ciudad Bolivia, 240 m (L. Lattke; P. S. Ward); *Bolívar*: Cuidad Bolívar (E. A. Klages); Rio Cuyuni, 66 km SSE El Dorado, 250 m (P. S. Ward); *Dto. Federal*: Camuri Grande, Pica "La Guardia" (A. Escalante); Caracas (N. A. Weber); Valle Camuri Grande, nr. La Guaira,70 m (I. Massin); *Guárico*: Altagracia de Orituco (C. R. F. Brandão & L.O.Campos; illegible); Est. Exp. Los Llanos, 27 km S Calabozo (C. R. F. Brandão); Hato Masaguaral (Y. D. Lubin); *Miranda*: Higuerote (K. Jaffé; G. Villegas); *Monagas*: Estacion Uverito (H. Romero); Uverito (C. J. Rosales & J. A. Gonzales); *Portuguesa*: El Oso (H. Romero); *Yaracuy*: San Felipe, El Peñón (C. Fuentes); *Zulia*: El Tucuco, Perija (R. W. Brook *et al.*); Maracaibo (E. Poirier; R. G. Wesson); *state unknown*: Akuriman (Anduze).

Pseudomyrmex eduardi (Forel)
(Figures 16, 17, 25)

Pseudomyrma eduardi Forel, 1912:29. Holotype (unique syntype) worker, Kingston, Jamaica (Forel) (MHNG) [Examined].

Worker measurements (n = 11).— HL 0.74–0.80, HW 0.50–0.57, MFC 0.009–0.018, CI 0.67–0.72, OI 0.53–0.59, REL 0.52–0.55, REL2 0.74–0.79, OOI 0.28–0.70, VI 0.79–0.86, FCI 0.017–0.032, SI 0.43–0.47, SI2 0.55–0.62, FI 0.46–0.53, PDI 0.93–1.31, MPI 0.039–0.073, NI 0.52–0.64, PLI 0.79–0.92, PWI 0.62–0.72, PPWI 1.19–1.50.

Worker diagnosis.— Similar to *P. caeciliae* (*q.v.*) in size, shape, and color; differing in sculpture– head largely smooth and shining, with scattered fine punctures (Fig. 25) which become coarser (but still somewhat effaced) in the region posterior to the compound eye; the punctulate-coriarious sculpture of the mesosoma is also somewhat effaced, producing rather strongly shining areas in the centre of the mesosoma dorsum and on the side of the propodeum; petiole, postpetiole, and gaster with a shinier appearance than in *P. caeciliae*, although still covered with moderately dense pubescence. Dark brown, the mandibles and tarsi lighter. Clypeus as in Figs. 16 and 17.

Comments.— This species is easily recognized by its combination of small size (HW <0.58), dark color, and smooth shiny appearance (especially on the head and mesosoma dorsum). The sculpture in the middle of the head between the compound eyes is particularly characteristic, consisting of very fine punctures and a few slightly coarser ones. All other species in the *P. oculatus* group have denser, coarser punctate sculpture on this part of the head.

Biology.— I collected colonies of *P. eduardi* in dead twigs of *Conocarpus erectus* and *Avicennia germinans* in mangrove in Venezuela. Other biological collection data include: in tree fall, wet forest (Costa Rica), dead stem of beach tree (Manaus, Brazil), in rain forest (Huánuco, Peru).

Material examined (CKIC, FFIC, INPA, IZAV, JTLC, KWJC, LACM, MCZC, MHNG, MNHN, MZSP, PSWC, USNM, WPMC, WWBC).—

BOLIVIA *Beni*: Cavinas (W. M. Mann); *La Paz*: Lower Rio Madidi (W. M. Mann); *Pando*: Abuna (W. M. Mann).

BRAZIL *AM*: Praia Grande, Rio Negro, Manaus (W. W. Benson); Rio Tarumá Mirim-Igapó (J. Adis); Tarumá-Mirim (J. Adis); km. 27, ZF–3, near Manaus (W. W. Benson); *MS*: Imbirussú-Corumbá (K. Lenko); *PA*: Tucurui (R. B. Neto; W. L. Overal); *RD*: "Jl-Paraná/Gleba G. II-Perdida" (J. Arías).

COLOMBIA *Cauca*: Popayán (W. & E. MacKay); *Cundinamarca*: Medina (F. Fernández); *Magdalena*: Gairaca, Parque Tayrona (C. Kugler); *Meta*: Carimagua, 370 m (M. Corn); Villavicencio (W. & E. MacKay).

COSTA RICA "Costa Rica" (P. Serre); *Heredia*: 3 km S Pto. Viejo, 50 m (J. T. Longino).

JAMAICA Kingston (A. Forel); St. Eliz., Pedro Cross, 230 m (J. T. Longino); St. James, Porto Bello, 75 m (J. T. Longino); Trelawny, Green Park, 0–150 m (J. T. Longino).

PANAMA *Panamá*: Matías Hernández (N. L. H. Krauss).

PERU *Huánuco*: Panguana, 220 m (M. Verhaagh).

VENEZUELA *Anzoátegui*: 1 km S El Hatillo, <5 m (P. S. Ward); *Aragua*: El Limon, 480 m (C. J. Rosales); *Bolívar*: Ciudad Bolivar (N. A. Weber); *Cojedes*: Jabillal (H. Romero); *Dto. Federal*: Caracas, Járdin Botánica (G. Morillo); *Guárico*: Est. Exp. Los Llanos, 27 km S Calabozo (C. R. F. Brandão); *Sucre*: 2 km W Cumana (D. H. Janzen); nr. Cumana (D. H. Janzen); *T. F. Delta Amacuro?*: "Orinoco Delta" (N. A. Weber).

Pseudomyrmex elongatus (Mayr)
(Figures 6, 14, 15, 20, 21)

Pseudomyrma elongata Mayr, 1870:413. Syntype worker, S. Fe de Bogota, Colombia (Schaufuss) (NHMV) [Examined]; here designated as LECTOTYPE.

Pseudomyrma elongata var. *tandem* Forel, 1906:228. Syntype workers, El Hiquito, near San Mateo, Costa Rica (P. Biolley) (MHNG) [Examined] [Synonymy by Creighton, 1955: 18; here confirmed].

Pseudomyrma alliodorae Wheeler, 1942: 157. Syntype workers, queen, Ancon, Canal Zone, Panama (W. M. Wheeler) (LACM, MCZC) [Examined]. One syntype worker in MCZC here designated LECTOTYPE. *Syn. nov.*

Pseudomyrma allidora Enzmann, 1945:77. Syntype workers, queen, Ancon, Canal Zone, Panama (W. M. Wheeler) (LACM, MCZC) [Examined] [Objective synonym of *P. alliodorae* Wheeler; Brown, 1949:42]

Worker measurements (n=55).— HL 0.73–0.93, HW 0.56–0.68, MFC 0.011–0.027, CI 0.66–0.79, OI 0.50–0.59, REL 0.53–0.59, REL2 0.73–0.82, OOI 0.04–0.67, VI 0.75–0.90, FCI 0.019–0.047, SI 0.42–0.48, SI2 0.54–0.63, FI 0.43–0.56, PDI 1.06–1.44, MPI 0.032–0.070, NI 0.54–0.65, PLI 0.79–1.09, PWI 0.62–0.87, PPWI 1.09–1.48.

Worker diagnosis.— Similar to *P. caeciliae* (*q.v.*), but averaging larger in size with longer eyes in relation to head length (Fig. 6; compare HW, HL, and REL); ocellar distance variable (OD/HW 0.097–0.165). Clypeus as in Figs. 14 and 15. Basal face of propodeum tending to be less elevated above level of mesonotum (compared to *P. caeciliae*) and usually meeting the declivitous face at a sharper angle. Head densely punctate and predominantly opaque; punctures on upper half of head mostly contiguous, separated by half their diameters or less (except for a thin shiny margin about 0.010 to 0.020 mm wide immediately posterior to the compound eye). Mesosoma punctate to coriarious-imbricate, the central areas more heavily sculptured and less shiny than in *P. caeciliae*.

Comments.— *P. elongatus* is a common and widespread species whose key features are its relatively small size (HW 0.56–0.68); densely punctate and

predominantly opaque head; long eyes (REL ≥ 0.53, REL2 ≥ 0.73); and relatively short, high petiole (PLI ≥ 0.79). Distinctions between it and *P. caeciliae*, *P. cubaensis*, and *P. urbanus* are discussed under those species.

I found the type worker of *P. elongatus*, which had previously eluded discovery (Ward, 1985), during a visit to NHMV. It had been misplaced under *Pseudomyrmex elongatulus* (Dalle Torre), a replacement name for the preoccupied *P. elongatus* (F. Smith, 1877), which is a markedly different species (see Kempf, 1967).

Biology.— This species is a generalist inhabitant of dead twigs of woody plants. It has been collected in mangroves, old fields, along roadsides, and in forested habitats ranging from tropical dry forest to secondary and primary rain forest. Specific nest-site records include dead twigs of *Avicennia germinans*, *Rhizophora mangle*, *Laguncularia racemosa*, *Baccharis halimifolia*, *Baccharis trinervis*, *Baccharis* sp., *Ficus* spp., *Vernonia patens*, *Terminalia catappa*, *Tecoma stans*, *Zanthoxylum culantrillo*, *Gliricidia sepium*, *Inga* sp., *Helicteres* sp., *Coccoloba* sp., and *Sapium* sp. Also I collected a colony in a live branch of *Pithecellobium saman*, and there are records from (apparently live) stems of *Cecropia*, *Cordia alliodora*, and *Triplaris cumingiana*. Thus, it appears that *P. elongatus* will occupy ant-plant domatia opportunistically.

Material examined (BMNH, CASC, CDAE, CELM, CNCC, CUIC, EBCC, FFIC, GCWC, ICCM, INPA, IZAV, JTLC, KWJC, LACM, MCSN, MCZC, MHNG, MZSP, NHMB, NHMV, PSWC, UCDC, USNM, UWEM, WPMC, WWBC).—

BELIZE El Cayo (N. L. H. Krauss).

BOLIVIA *Beni*: 46 km SSW San Borja, 300 m (P. S. Ward); Est. Biol. Beni, 42 km E San Borja, 210 m (P. S. Ward); Huachi (W. M. Mann); Reyes (W. M. Mann); *La Paz*: Espia Rio Bopi (W. M. Mann); Sta. Helena (W. M. Mann).

BRAZIL *AC*: Porto Valter (*P. L. Herbst*); *AM*: Arquipelago d. Anavilhanas, Rio Negro (c.u.); Faz. Dimona, 80 km N Manaus, 80 m (P. S. Ward); High Falls, Rio Taruma (W. L. Brown); Ig. Marianil, Rio Branco Rd., 24 km NE Manaus (W. L. Brown); Manaus (C. R. Gonçalves; c.u.); Manaus, 60 m (P. S. Ward); Manaus-AM.010, km. 10 (A. Y. Harada); Praia Grande, Rio Negro, Manaus (W. W. Benson); Reserva Ducke (J. A. Rafael); Reserve Ducke, NE of Manaus (W. L. Brown); Rio Tarumá Mirim-Igapó (J. Adis); Tarumá-Mirim (J. Adis); km. 24, ZF–3, near Manaus (W. W. Benson); km. 27, ZF–3, near Manaus (W. W. Benson); *BA*: Salvador (N. L. H. Krauss); *ES*: Linhares (M. Alvarenga); *GO*: Araguacema (J. A. Rafael); Jatai (F. M. Oliveira); *MA*: Bacabal (W. W. Kempf); *MG*: Pedra Azul, 800 m. (Seabra & Alvarenga); *MS*: Faz. Canàa, Três: Lagoas (F. Lane); Faz. Floresta, Mun. Três: Lagoas (Exp. Depto. Zool.); Imbirussú-Corumbá (K. Lenko); Ladário (Gilbert & Müller); Serra do Urucum, Corumbá (K. Lenko); Três Lagoas (Exp. Depto. Zool.; K. Lenko); *MT*: Sinop (Alvarenga & Roppa; M. Alvarenga); *MT?*: "Matto Grosso" (Germain); *PA*: Belém (P. Vanzolini; c.u.); Belém–Tapaná (A. Y. Harada); C. Araguaía (A. Y. Harada; J. A. Rafael); C. Araguaía, Campo Gramado (A. Y. Harada); Cach. (do) Breu (Sampaio); Igarapé-Açu (c.u.); Oriximiná, Alcoa Miner. M. Branco (A. Y. Harada); Oriximiná-Rio Trombetas, Alcoa Miner. Campina (A. Y. Harada); Sa. dos Carajás (25 km W Camp N–1) (W. W. Benson); Santarém, Taperinha (R. L. Jeanne); Tucurui (R. B. Neto; W. L. Overal); Utinga track, nr. Belém (K. Lenko); *PE*: Tapera (B. Pickel); *RD*: Porto Velho (C. R. Gonçalves); Vilhena (M. Alvarenga); *RJ*: Cabo Frio (C. Gilbert); Fonseca, Niterói (C. R. Gonçalves); Guaratiba (A. Silva); I. Governador (C. R. Gonçalves); Marambaia (R. Müller); Rio de Janeiro, Taquara (T. Borgmeier); São Bento (P. A. Telles); "Guanabara dos Bandeirantes" (N. L. H. Krauss); *SP*: Adolfo ("P. de preia Rio Tietê") (M. Dimiz); Agudos (C. Gilbert; R. Müller); Anhembi, Faz. Barr. Rico (W. W. Kempf *et al.*); Barabosa-Tietê (J. Diniz [= missp. of M. Dimiz?]); Cachoeira das Emas (EEBP, Mun. Piraçununga (W. L. Brown); Campinas (W. W. Benson); Faz. Itaquerê, Nova Europa (K. Lenko); Franca (c.u.); S. Sebastião (Fleddermann; W. W. Kempf); Ubatuba (P. C. Montouchet); *state unknown*: Chapada (c.u.).

COLOMBIA *Bolívar*: Cartagena (c.u.); *Cauca*: 15 mi. S Corinto, 1140 m (E. I. Schlinger & E. S. Ross); *Cundinamarca*: "S. Fe de Bogota" (Schaufuss); Anapoima (I. Zenner); El Colegio & Anapoima (I. Zenner); *Guajira*: Puente Bomba, nr. Dibulla (W. L. & D. E. Brown); Rio Don Diego (C. Kugler & W. L. Brown); Serrania de Macuira, W. of Nazareth (C. Kugler & W. L. Brown); *Huila*: 10 km S Campoalegre (W. & E. MacKay); 10 km. SE Hobo (W. & E. MacKay); 10 km. W Palermo (W. & E. MacKay); 1 km S Neiva (W. & E. MacKay); 4 km. S Tello (W. & E. MacKay); Colombia (W. & E. MacKay); La Plata (W. & E. MacKay); Palermo (W. & E. MacKay); *Magdalena*: 2 km E Orihueca, 20 m (P. S. Ward); 2 km ESE Minca, 780 m (P. S. Ward); 5 km SE Rio Frio, 100 m (P. S. Ward); Bahia de Gairaca, Tayrona Pk, 20 km NE Santa Marta (H.-G. Müller); Cañaveral, 50 m (P. S. Ward); Cañaveral, 5 m (P. S. Ward); Cañaveral, <5 m (P. S. Ward); Digrera, base of mts. nr. Santa Marta (C. Kugler & W. L. Brown); Minca (W. L. Brown); Rio Frio (Darlington); Rio Frio, 20 m (P. S. Ward); Villa Culebra, nr. Bonda, 10 km E Sta. Marta (H.-G. Müller); *Magdalena?*: locality illegible (A. Forel); *Meta*: Reserva Macarena, 560 m (F. Fernández); Reserva Macarena, Caño La Curia, 580 m (F. Fernández); *Valle*: 6 km S Univ. Valle (W. L. Brown); Cali (N. L. H. Krauss); Cali, in quarantine at San Francisco (c.u.); Dagua (W. & E. MacKay).

COSTA RICA "Costa Rica" (Alfaro; P. Biolley); *Alajuela*: 11 mi. N Florencia (D. H. Janzen); El Hiquito near San Mateo, 250 m (P. Biolley); *Guanacaste*: 1 km SW Pto. Coyote, <5 m (P. S. Ward); 4 km N Cañas (D. H. Janzen); *Heredia*: 10°20'N, 84°04'W, 500 m (J. T. Longino); 3 km S Pto. Viejo, 50 m (J. T. Longino); F. La Selva, 3 km S Pto. Viejo (H. A. Hespendeide); Finca La Selva (D. H. Janzen); *Limón*: La Lola (D. H. Janzen; M. J. Stelzer; N. A. Weber); Zent (F. Lara); *Puntarenas*: 14 km E Palmar Norte, 120 m (P. S. Ward); 14 km E Palmar Norte, 70 m (P. S. Ward); 1 km NE Tárcoles, 20 m (P. S. Ward); 5 km N Ciudad Neily, 780 m (P. S. Ward); Golfito, 5 m (P. S. Ward); Guaria, 700 m (J. T. Longino); Llorona, Corcovado Natl. Pk. (J. T. Longino); Llorona, Corcovado Natl. Pk., 10 m (P. S. Ward); Manuel Antonio Natl. Pk., 5 m (P. S. Ward); Manuel Antonio Natl. Pk., <5 m (P. S. Ward); Monteverde, 1100 m (P. S. Ward); Monteverde, 1200 m (P. S. Ward); Osa Penin., Corcovado Natl. Pk. (J. T. Longino); Palmar Sur (D. H. Janzen); Reserva Biol. Carara, 10 m (P. S. Ward); Reserva Biol. Carara, 500 m (P. S. Ward); Sirena, Corcovado Natl. Pk. (J. T. Longino); *San José*: 3.5 km NE Santiago de Pur (D. H. Janzen); 40 km S San Isidro de General (D. H. Janzen).

ECUADOR *Manabí*: Puna Island (Ross & Michelbacher); *Pichincha*: 6 mi W Santo Domingo de los Colorados (E. I. Schlinger & E. S. Ross).

EL SALVADOR San Salvador (N. L. H. Krauss); Santa Anna (N. L. H. Krauss).

GUATEMALA "Guatemala", quarantine San Francisco (c.u.); *Escuintla*: Escuintla (W. M. Wheeler); *Escuintla?*: San José (E. S. Ross; E. I. Schlinger & E. S. Ross); *Guatemala*: Guatemala City, quarantine San Francisco (c.u.); *Petén*: Tikal (N. L. H. Krauss); *Retalhuleu*: 1.3 mi E Champerico (D. H. Janzen); 5 mi W Retalhuleu, Hwy. CA–2, at Rio Nil (D. H. Janzen).

GUYANA *Mazaruni-Potaro*: Kartabo, Bartica Dist. (W. M. Wheeler); *North West*: Wauna & Tokomabu (J. G. Myers); *Rupununi*: Dadanawa, 100 m (J. T. Longino).

MEXICO *Is. Tres Marias*: Maria Magdalena I. (H. H. Keifer; R. R. Snelling); *Jal.*: 14 km SSE Chamela, 20 m (P. S. Ward); 2 km E Chamela, 20 m (P. S. Ward); 32.8 mi. SW Autlán (D. H. Janzen); 6 km NW El Tuito, 560 m (P. S. Ward); *Mor.*: Cocoyotla, munic. Coatlan del Rio, 1120 m (G. Alemán); Cuzuhuatlán (G. Alemán); Los Alcanfores, Mpo. Xochitepec (G. Alemán); Tetecala, 800 m (G. Alemán); *Oax.*: 19 km N San Pedro Pochutla, 200 m (W. P. MacKay); *S.L.P.*: Rio Amahac, Tamazunchale, 300 ft. (W. S. Creighton); Tamazunchale (W. S. Ross); *Sin.*: 4.6 mi E Chupaderos (E. I. Schlinger); Ver.: Cotaxtla Exp. Sta, Cotaxtla (D. H. Janzen); *Yuc.*: 11 km S Progreso (E. O. Wilson).

NICARAGUA *Matagalpa*: El Tuma, 30 km E Matagalpa (C. Kugler & J. Hahn).

PANAMA *Bocas del Toro*: Changuinola Dist. (G. C. Wheeler); *Canal Zone*: 2 km W Gamboa, 30 m (P. S. Ward); 5 km WNW Gatun Dam, 160 m (P. S. Ward); 6 km NW Gamboa, 50 m (P. S. Ward); 6 km NW Gatun Dam, 75 m (P. S. Ward); Ancon (W. M. Wheeler); Barro Colorado I. (W. L. Brown & E. S. McCluskey; H. Wolda; G. C. Wheeler; J. Zetek); Cerro Galera, 9 km W Panama City, 200 m (W. L. Brown *et al.*); Chiva Chiva (N. L. H. Krauss); Fort Sherman, Island P2 (D. Simberloff); Frijoles (G. C. Wheeler; W. M. Wheeler); Miraflores (W. M. Wheeler); Ruta 1, 14 km W Panama City, 100 m (W. L. Brown *et al.*); Ruta 1, Howard AFB, W of Panama City, 50 m (W. L. Brown *et al.*); vic. Pta de los Chivos, 3 km SW Gatun, 100 m (W. L. Brown *et al.*); *Chiriqui*: "Prov.Chiriqui" (F. M. Gaige); 10.7 mi ESE La Concepción (D. H. Janzen); *Colón*: Colón (E. Adams); *Panamá*: Bella Vista (W. M. Wheeler); Cerro Azul, 800 m (E. Mockford); Isla San José, Islas Perlas (C. Campbell); Matías Hernández (N. L. H. Krauss); Pueblo Nuevo (W. M. Wheeler); Rio Piedras (D. H. Janzen); *Veraguas*: 0.3 mi SW Santiago (D. H. Janzen); *prov.unknown*: "Lilihe R" (W. M. Wheeler).

PERU *Madre de Dios*: 30 km SW Pto. Maldonado, 290 m (T. L. Erwin *et al.*); Cocha Cachu, Rio Manu (D. Hunt); *San Martín*: Convento, 26 km NNE Tarapoto, 220 m (P. S. Ward); La Perla, 21 km NNE Tarapoto, 220 m (P. S. Ward); Tarapoto, 350 m (P. S. Ward).

TRINIDAD Maracas Valley (N. A. Weber).

UNITED STATES *Florida*: *Collier Co.*: 6 mi S Naples (G. S. Walley); Everglade[s] (W. T. Davis); *Dade Co.*: no specific locality (J. N. Knull); Cocoanut Grove (c.u.); Miami (c.u.); Miami, 10 m (P. S. Ward); Rattlesnake Hammock, Homestead (R. Gregg); Shark Valley, Everglades Natl. Pk. (P. S. Ward); *Highlands Co.*: Archbold Biol. Stn., L. Placid (T. C. Schneirla); *Lee Co.*: Ft. Myers (W. M. Barrows; D. E. Read); *Monroe Co.*: Big Pine Key (E. O. Wilson); John Pennekamp St. Pk., <5 m (P. S. Ward); Key Largo (A. Wetmore; c.u.); Key West (E. A. Schwartz); Lower Matecumbe Key (J. R. Vockeroth); N. Key Largo (R. W. Klein); Plantation Key (E. O. Wilson).

VENEZUELA "Venezuela", in quarantine at San Francisco (c.u.); *Aragua*: El Limon, 450 m (C. J. Rosales); El Limon, 480 m (C. J. Rosales); *Barinas*: 17 km SSW Ciudad Bolivia, 240 m (P. S. Ward); 17 km SW Ciudad Bolivia, 240 m (P. S. Ward); *Bolívar*: 49 km ENE Tumeremo, 200 m (P. S. Ward); *Carabobo*: Puerto Cabello (W. L. Brown); *Cojedes*: 20 km W San Carlos (W. L. Brown); *Dto. Federal*: La Pastora, Caracas (c.u.); La Trinidad, Caracas (M. E. Lopez); *Guárico*: Altagracia de Orituco (C. R. F. Brandão & L. O. Campos); Hato Masaguaral (Y. D. Lubin); *Merida*: Merida (A. S. Menke & D. Vincent); *T. F. Amazonas*: P. N. Duida–Marahuaka, Culebra, 250 m (K. Jaffé); *T. F. Delta Amacuro*: Palo Blanco (H. Romero); *T. F. Delta Amacuro?*: "Orinoco Delta" (N. A. Weber); *Trujillo*: 19 km E Boconó, 600 m (J. T. Longino; P. S. Ward); *Zulia*: El Tucuco, Perija (R. W. Brooks *et al.*).

Pseudomyrmex oculatus (F. Smith)
(Figure 7)

Pseudomyrma oculata Smith, 1855:159. Two syntype workers, Santarém, Brazil (Bates) (BMNH) [Examined]. One syntype worker here designated LECTOTYPE.

Pseudomyrma advena F. Smith, 1855:157. [Objective synonym of *P. oculatus*; Forel, 1911:277. See discussion by Forel (1911) and Kempf (1961)].

Pseudomyrma dolichopsis Forel, 1899:87. Syntype workers, Suerre, Jimenez, Costa Rica (Alfaro) (MHNG, MCSN) [Examined] [Synonymy by Kempf, 1961:375; here confirmed].

Pseudomyrma dolichopsis var. *implicata* Forel, 1911:277. Two syntype workers, Amazonas (Bates) (MHNG) [Examined] [Synonymy by Kempf, 1961:375; here confirmed]. One syntype worker here designated LECTOTYPE (see comments below).

Pseudomyrma sericea var. *altinoda* Mann, 1916:427. Syntype workers Porto Velho, Rio Madeira, Brazil (Mann & Baker) (MCZC) [Examined] *Syn. nov.*

Pseudomyrma wessoni Enzmann, 1945:97. Syntype queen, Peru, (MCZC) [Examined] *Syn. nov.*

Pseudomyrma wessoni var. *tuberculata* Enzmann, 1945:98. Holotype worker, Peru [Not examined] *Syn. nov.*

Pseudomyrmex oculatus (F. Smith); Kempf, 1961:375 [Redescription of worker and queen].

Worker measurements (n=24).— HL 0.94–1.09, HW 0.73–0.91, MFC 0.017–0.031, CI 0.77–0.87, OI 0.57–0.61, REL 0.55–0.62, REL2 0.67–0.78, OOI (–0.20)–0.37, VI 0.72–0.81, FCI 0.021–0.037, SI 0.46–0.50, SI2 0.62–0.72, FI 0.40–0.44, PDI 0.97–1.40, MPI 0.032–0.056, NI 0.72–0.81, PLI 0.86–1.01, PWI 0.66–0.82, PPWI 1.35–1.61.

Worker diagnosis.— Medium to large species, for the *oculatus* group (HW 0.73–0.91), with broad head (CI 0.77–0.87) and with large, elongate eyes which tend to protrude conspicuously from the sides of the head and which typically (but not always) reach the level of the median ocellus, when head is held in full-face view; occipital margin flat to moderately concave; funicular segments II and III about as long as broad, or nearly so. Fore femur relatively slender (FI 0.40–0.44); metanotal groove moderately impressed; basal face of propodeum flat to weakly convex (lateral view), conspicuously elevated anteriorly above level of mesonotum; basal face of propodeum usually exceeding length of the declivitous face and rounding into the latter, which is laterally submarginate. Petiolar node (Fig. 7) high and subangulate, with distinctive lateral profile: anterior face smoothly continuous with the flattened, posteriorly uplifted dorsal face which itself rounds sharply into the vertical posterior face; anteroventral petiolar process conspicuous, variable in shape (from bluntly rounded to slightly recurved and hook-like); postpetiole broader than long, in lateral view appearing rather high, with the convex, gradually ascending anterodorsal face rounding into a more

steeply descending posterior face.

Head densely punctate and typically opaque; becoming sublucid on upper third of head in some individuals, because of shiny interspaces between some of the punctures. Mesosoma punctate to coriarious-imbricate and predominately opaque; petiole, postpetiole, and gaster subopaque, covered with numerous fine piligerous punctures. Erect pilosity and appressed pubescence common on most of body, including mesosoma dorsum. Medium to dark brown, the antennae, tibiae, and tarsi variably lighter, often contrastingly so; pronotum and parts of head sometimes lighter in color than gaster; mandibles pale luteous.

Comments.— This common, widely distributed species shows considerable geographical variation (particularly in size, sculpture, color, and head shape), but it is at once recognizable by the distinctive shape of the petiolar node. The sudden, subangulate juncture of the dorsal and posterior faces of the node (Fig. 7) is seen in no other related species. Also characteristic of *P. oculatus* are the elongate eyes (see REL and REL2 values), relatively broad head, the (typically) punctate-opaque sculpture of the head, and the shape of the postpetiole in lateral view (summit of postpetiolar node displaced posteriorly relative to other species in the *P. oculatus* group, except *P. schuppi*).

Lectotypes of both *P. oculatus* and *P. implicatus* are designated because the apparent type series of these taxa contain more than one species. In the BMNH, under *P. oculatus*, I found three species: (1) two syntype workers of what is here interpreted to be *P. oculatus*, from Santarem, Brazil; (2) an alate queen of *P. peperi* (Forel), a Central American acacia-ant labelled (obviously erroneously) "Santarem"; and (3) four workers of *P. filiformis*, two of which (from Villanova, Brazil) were labelled as types of *P. oculatus*. The type series of *P. implicatus* in MHNG contains two species: (1) two workers of *P. oculatus*; and (2) one worker of *P. curacaensis*. For nomenclatural stability I have chosen as lectotypes of *P. oculatus* and *P. implicatus* those workers which correspond to the species described (at least as a queen) and illustrated (as a worker, under the name *P. advena*) by F. Smith (1855). The choice of lectotypes is also consistent with Kempf's (1961) concept of *P. oculatus*, which was based on an examination of material in the Hope Collection, Oxford (OXUM) which Kempf considered to represent part of the type series of *P. oculatus*.

The syntype queen of *P. wessoni* (Enzmann) is clearly conspecific with *P. oculatus*. Unfortunately, the type of *P. wessoni tuberculatus* (Enzmann) cannot be located, and second-guessing the identity of Enzmann's creations is an unsatisfying task. Nevertheless there are enough features of the original description (broad head; large eyes; densely punctate, opaque head; petiolar profile similar to that of *P. wessoni*) to support synonymy under *P. oculatus*.

Biology.— *P. oculatus* is typically found nesting in dead twigs or branches, in rain forest or at the edge of rain forest, less frequently in open or drier habitats. Specific nest-site records include dead twigs of *Ficus, Hampea, Inga, Vochysia,* and various unidentified lianas; I found one colony in the dead leaf sheath of a *Scheelea* palm.

Material examined (BMNH, CASC, CNCC, CUIC, FFIC, GCWC, GHPC, ICCM, INPA, JTLC, KSUC, LACM, MCSN, MCZC, MHNG, MZSP, PSWC, UCDC, USNM, UWEM, WWBC).—

BELIZE Belize (c.u.); San Ignacio, Cayo, 60 m (S. E. Schoenig); Manatee (J. D. Johnson).

BOLIVIA *Beni*: 45 km SSW San Borja, 270 m (P. S. Ward); 46 km SSW San Borja, 300 m (P. S. Ward); Cavinas (W. M. Mann); Est. Biol. Beni, 42 km E San Borja, 210 m (P. S. Ward); Ivon (W. M. Mann); *La Paz*: Covendo (W. M. Mann); Ixiamas (W. M. Mann); Sta. Helena (W. M. Mann).

BRAZIL *AC*: Rio Branco (M. Alvarenga); *AM*: "Amazonas" (Bates); "Faz. NAFG, Est. Mr. Carac. km. 31" (c.u.); Arquipelago Anavilhanas, Rio Negro (R. Negrett); Benjamin Constant & vicinity (W. L. Brown); Cucuí, Ponto 08 (D. Dias); E.E.S.T., km. 44, BR-174, [near] Manaus (c.u.); Faz. Dimona, 80 km N Manaus, 80 m (P. S. Ward); Faz. Esteio, 80 km NNE Manaus, 80 m (P. S. Ward); Humaita (P. da Silva & D. Araujo); Ig. Jaraqui, Marg. esq., Rio Negro (Exp. Depto. Zool.); Ig. Marianil, Rio Branco Rd., 24 km NE Manaus (W. L. Brown); Manaus (A. Y. Harada; K. Lenko); Manaus-Caracaraí, km. 61 (W. W. Benson); Praia Grande, Rio Negro, Manaus (W. W. Benson); Reserva Ducke, NE of Manaus (W. L. Brown); Rio Taruma Mirim-Igapó (J. Adis); km. 24, ZF-3, Faz. Esteio, near Manaus (A. Y. Harada); km. 24, ZF-3, near Manaus (W. W. Benson; A. Y. Harada); km. 27, ZF–3, near Manaus (W. W. Benson); km. 44, BR-174, near Manaus (W. W. Benson); km. 44.5, BR-174, near Manaus (W. W. Benson); *BA*: Una (M. C. Alves); *ES*: Linhares (M. Alvarenga); *GO*: Araguacema (A. Y. Harada; J. A. Rafael); Jatai (F. M. Oliveira); *MT*: Barra do Tapirapé (B. Malkin); Sinop (Alvarenga & Roppa; M. Alvarenga); Utiariti, Rio Papagaio, 325 m (Lenko & Pereira); Vila Vera (M. Alvarenga); Xingu (Alvarenga & Werner); *PA*: "Pará" (Schulz.); Belém (K. Lenko; N. Rosa); Belém-Tapaná (A. Y. Harada); C. Araguaía (A. Y. Harada; J. A. Rafael); Cach. Breu (Sampaio); Caldeirao, R. Itacaiunas (C. R. F. Brandão & W. W. Benson); Jacareacanga (M. Alvarenga); Oriximiná (A. Y. Harada); Oriximiná, Alcoa C. Alta (A. Y. Harada); S. Norte, Carajás (C. R. F. Brandão & W. W. Benson); Sa. dos Carajás (W. W. Benson); Santarém (Bates); Tucurui (W. L. Overal); Utinga tract, nr. Belém (P. F. Darlington); *RD*: Porto Velho (J. Arías); Porto Velho, Rio Madeira (W. M. Mann & Baker); Rio Madeira, Madeira-Mamore R. R. Co. Camp 39 (W. M. Mann & Baker); S. Antonio de Guaporé (c.u.); Vilhena (M. Alvarenga; A. Y. Harada); *RR*: Rio Uraricuíra leha Manicá (R. Negrett).

COLOMBIA *Cundinamarca*: Medina (F. Fernández); *Magdalena*: 2 km ESE Minca, 780 m (P. S. Ward); Naranjo (A. Forel).

COSTA RICA "Costa Rica" (Tonduz); *Alajuela*: 11 mi N Florencia (D. H. Janzen); *Cartago*: Turrialba (D. H. Janzen); *Guanacaste*: 12 km N Liberia (D. H. Janzen); Finca Taboga, 6 mi. S, 6 mi. W Cañas (D. H. Janzen); *Heredia*: 10°20'N, 84°04'W, 500 m (J. T. Longino); F. La Selva, 3 km S Pto. Viejo (H. A. Hespenheide); P. N. Braulio Carrillo, 500 m (J. T. Longino); *Limón*: Estrella Valley (G. C. Wheeler); Hamburg Farm, Santa Clara (F. Nevermann); Jiménez (Alfaro?); La Lola (N. A. Weber); Limón (N. L. H. Krauss); Matina (A. Alfaro); Moin (D. H. Janzen); Parismina Br., Santa Clara (F. Nevermann); Portete (D. H. Janzen); Suerre, Jiménez (Alfaro?); *Puntarenas*: 1 km NE Tárcoles, 20 m (P. S. Ward); 1 km N Palmar Sur (D. H. Janzen); 20 km NE Palmar Sur (D. H. Janzen); 1–5 mi. NW Rincon (D. H. Janzen); Golfito (W. S. Ross; Truxal & Menke); Llorona, Corcovado Natl. Pk., 100 m (P. S. Ward); Llorona, Corcovado Natl. Pk., 10 m (P. S. Ward); Llorona, Corcovado Natl. Pk. (J. T. Longino); Manuel Antonio Natl. Pk. (L. Masner); Manuel Antonio Natl. Pk., 10 m (P. S. Ward); Manuel Antonio Natl. Pk., 20 m (P. S. Ward); Manuel Antonio Natl. Pk., 5 m (P. S. Ward); Manuel Antonio Natl. Pk., <5 m (P. S. Ward); Reserva Biol. Carara, 40 m (P. S. Ward); Reserva Biol. Carara, 500 m (P. S. Ward); Sirena, Corcovado Natl. Pk. (J. T. Longino); Sirena, Corcovado Natl. Pk., 0–100 m (J. T. Longino); Sirena, Corcovado Natl. Pk., 50 m (J. T. Longino); *San José*: 3.5 km NE Santiago de Pur (D. H. Janzen); 40 km S San Isidro de General (D. H. Janzen).

ECUADOR *prov. unknown*: Piedrero (M. Deyrup).

FRENCH GUIANA Cayenne (Pillault); Saül (G. H. Perrault).

GUATEMALA *Alta Verapaz*: Cacao Trece Aguas (Barber & Schwarz); *Izabal*: Lago Izabal, 1.5 km NE El Estor (D. H. Janzen); *Suchitepéquez*: Moca (W. M. Wheeler).

GUYANA *East Demerara - West Coast Berbice*: Timehri, 0–50 m (J. T. Longino); *Mazaruni-Potaro*: Bartica (W. Beebe); Kartabo, Bartica Dist. (W. M. Wheeler); Oko R., Cuyuni trib. (N. A. Weber); *Rupununi*: Karanambo, 100 m (J. T. Longino); Tutwau V., 100–300 m (J. T. Longino).

HONDURAS *Atlántida*: La Ceiba (F. J. Dyer); Tela (W. M. Mann); *Colón*: Corocito (c.u.); *Cortés*: Lago Yojoa, 680 m (W. L. Brown).

MEXICO *Chis.*: 10 km S Palenque (M. Arrendondo); *Q. Roo*: San Miquel, Cozumel I. (N. L. H. Krauss); Vallarta (A. Dejean); *Tabasco*: 3 mi. W Cardenas (D. H. Janzen); *Ver.*: "St. Lucrecia, Teh." (W. M. Mann); 6 mi. NW Salinas (E. Schlinger); Los Tuxtlas (R. L. Jeanne); Los Tuxtlas, 10 km NNW Sontecomapan, 200 m (P. S. Ward); Los Tuxtlas, 10 km NNW Sontecomapan, 500 m (P. S. Ward).

NICARAGUA *Matagalpa*: El Tuma, 30 km E Matagalpa (C. Kugler & J. Hahn).

PANAMA *Canal Zone*: 3 km WNW Gamboa, 60 m (P. S. Ward); 5 km WNW Gatun Dam, 160 m (P. S. Ward); 6 km NW Gamboa, 50 m (P. S. Ward); Barro Colorado I. (N. Banks; W. L. Brown & E. S. McCluskey; H. Emerson; P. B. Kannowski, R. B. Root & W. L. Brown; R. B. & L. S. Kimsey; J. Reiskind; C. W. Rettenmeyer; W. M. Wheeler; H. Wolda; c.u.); Cerro Galera, 9 km W Panama City, 200 m (W. L. Brown *et al.*); Fort Kobbe (C. Campbell); Frijoles (W. M. Wheeler); Margarita Swamp (J. Zetek); Puma Island (R. B. Kimsey); vic. Pta de los Chivos, 3 km SW Gatun, 100 m (W. L. Brown *et al.*); Summit (N. L. H. Krauss); *Chiriqui*: Progreso (F. M. Gaige); *Darién*: Cana, 500 m (D. M. Olson); *Panamá*: Bella Vista (N. Banks); Cerro Campana, 800–950 m (G. B. Fairchild & W. L. Brown).

PERU "Peru" (c.u.); *Junín*: Chanchamayo, Anashirone R. (C. A. Portocarrero); El Campamiento, Col. Perené (J. C. Bradley); Satipo (W. F. Walsh); *Loreto*: 15 km WSW Yurimaguas, 200 m (P. S. Ward); Yurac, 67 mi E Tingo Maria (E. I. Schlinger & E. S. Ross); *Madre de Dios*: 30 km SW Pto. Maldonado, 290 m (T. L. Erwin *et al.*); *San Martín*: Convento, 26 km NNE Tarapoto, 220 m (P. S. Ward); Davidcillo, 30 km NNE Tarapoto, 220 m (P. S. Ward).

TRINIDAD "Trinidad" (N. A. Weber; c.u.); Nariva Swamp (N. A. Weber); Palo Seco (H. Morrison).

VENEZUELA *Barinas*: 17 km SSW Ciudad Bolivia, 240 m (P. S. Ward); *Bolívar*: 44 km ENE Tumeremo, 200 m (P. S. Ward); Campamento Rio Grande, 250 m (P. S. Ward); Rio Cuyuni, 66 km SSE El Dorado, 250 m (P. S. Ward); *Carabobo*: San Esteban (W. L. & D. E. Brown); *T. F. Delta Amacuro?*: "Orinico Delta" (N. A. Weber).

Pseudomyrmex pisinnus sp. nov.
(Figures 11a, 11b)

Holotype worker.— BRAZIL, *SP*: Monte Aprazível, Faz. Bacuri [20°45'S, 49°42'W], 19.vii.1974, in *Eupatorium* stem, M. Dimiz, no. 644 (MZSP). HW 0.51, HL 0.78, EL 0.41, PL 0.30, PH 0.22.

Paratypes.— Same data as holotype, four workers (LACM, MCZC, MZSP, PSWC). Additional, non-paratypic material is listed below.

Worker measurements (n=8).— HL 0.75–0.78, HW 0.47–0.51, MFC 0.009–0.016, CI 0.61–0.68, OI 0.49–0.55, REL 0.52–0.54, REL2 0.78–0.86, OOI 0.73–1.58, VI 0.76–0.87, FCI 0.018–0.033, SI 0.41–0.45, SI2 0.50–0.54, FI 0.46–0.52, PDI 1.46–1.69, MPI 0.029–0.047, NI 0.59–0.64, PLI 0.67–0.77, PWI 0.54–0.65, PPWI 1.07–1.20.

Worker diagnosis.— Very small species (HW 0.47–0.51) with elongate head (Fig. 11a; CI 0.61–0.68), and short scapes relative to eye length (SI2 0.50–0.54); sides of head subparallel; occipital margin flat to slightly concave, in frontal view; funicular segments II and III notably broader than long (FLI 1.16–1.48, n=4). Fore femur broad; metanotal groove rather weakly impressed; basal face of propodeum rounding into the much shorter declivitous face. Petiolar node (Fig. 11b) rather long and low, the dorsum broadly rounded in lateral profile (PLI 0.67–0.77); postpetiole about as broad as long.

Head sublucid, covered with numerous piligerous punctures; punctures relatively coarse but appearing somewhat effaced, and separated (at least on the upper half of the head) by shiny interspaces of one or more diameters' distance, especially in the region immediately posterior to the compound eye. Mesosoma weakly punctate to coriarious–imbricate, sublucid dorsally. Petiole, postpetiole, and gaster subopaque to sublucid, covered with numerous, fine piligerous punctures. Erect pilosity and appressed pubescence present on most of the body; erect hairs present on the pronotum, mesonotum and propodeum, but relatively short, sparse, and inconspicuous, except for one pair on the pronotal shoulders and a second pair above the juncture of the basal and declivitous faces of the propodeum. Body light orange-brown to yellow-brown, with darker infuscation on the anterior third of the first gastric (fourth abdominal) tergite, on the succeeding gastric tergites, and on part of the hind femur; mandibles paler luteous.

Comments.— This small, slender species is easily recognized by the combination of small size, elongate head, long basal face of propodeum, and low petiole (see worker key and description above). The short scapes (relative to head length), sublucid appearance, and light orange-brown color are also distinctive.

Biology.— The type series was collected in a dry stem of *Eupatorium* sp. The Peruvian specimens are from primary rain forest.

Material examined.— Type material listed above plus the following (USNM, PSWC):

PERU *Huánuco*: Panguana, 220 m, 9°37'S, 74°56'W (M. Verhaagh); *Madre de Dios*: Rio Tambopata Res., 30 km SW Pto. Maldonado, 290 m, 12°50'S, 69°20'W (T. L. Erwin *et al.*).

Pseudomyrmex schuppi (Forel)
(Figure 8)

Pseudomyrma schuppi Forel, 1901a:298. Syntype workers, São Leopoldo, Rio Grande do Sul, Brazil (Schupp) (MCSN, MZSP, NHMV) [Examined].

Pseudomyrma schuppi var. *confusior* Forel, 1901a:299. Syntype workers, Rio Grande do Sul, Brazil (Schupp) (MHNG) [Examined] [Synonymy by Kempf, 1961:380; here confirmed].

Pseudomyrma schuppi var. *geraensis* Forel, 1912:23. Syntype workers, Juiz de Fora, Minas Gerais, Brazil (Sampaio) (MHNG) [Examined] [Synonymy by Kempf, 1961:380; here confirmed].

Pseudomyrmex schuppi (Forel); Kempf, 1961:380 [Differentiating characters of worker and queen.]

Worker measurements (n = 14).— HL 0.96–1.18, HW 0.82–0.93, MFC 0.023–0.038, CI 0.79–0.88, OI 0.55–0.64, REL 0.52–0.56, REL2 0.62–0.67, OOI 0.23–0.60, VI 0.75–0.84, FCI 0.026–0.042, SI 0.45–0.48, SI2 0.68–0.76, FI 0.39–0.45, PDI 1.16–1.34, MPI 0.037–0.053, NI 0.53–0.62, PLI 0.94–1.07, PWI 0.85–0.99, PPWI 1.32–1.60.

Worker diagnosis.— Relatively large species (HW 0.82–0.93), with broad head (CI 0.79–0.89), and eyes of moderate size; sides of head broadly convex, rounding into the occipital margin which varies from flat to slightly concave; funicular segments II and III about as long as broad (FLI 1.71–2.12, n=9). Fore femur, metanotal groove, propodeum, and postpetiole similar to those of *P. oculatus* (*q.v.*), except basal and declivitous faces of propodeum tend to be more clearly differentiated. Petiolar node (Fig. 8) high and broadly rounded in lateral view (PLI 0.94–1.07), very broad in dorsal view (PWI 0.85–0.99), with relatively strong dorsolateral margination; anteroventral process of petiole conspicuous, tooth–like, often bluntly recurved.

Head densely punctate, opaque; mesosoma obscurely punctate to coriarious–imbricate, opaque to subopaque; petiole, postpetiole, and gaster subopaque, covered with numerous fine piligerous punctures. Erect pilosity and appressed pubescence common and conspicuous on most parts of the body including the mesosoma dorsum. Body medium to dark brown, the antennae and tarsi (and sometimes mandibles and promesonotum) lighter in color.

Comments.— *P. schuppi* is diagnosed minimally by its relatively large size (HW > 0.81) and high, broad petiole (PLI > 0.93, PWI > 0.84) whose dorsum is smoothly rounded in lateral profile. Also characteristic of *P. schuppi* are the conspicuous elevation of the basal face of the propodeum above the level of the mesonotum and the posterior displacement of the postpetiolar node as seen in lateral view. These last two features are shared with *P. oculatus*, from which *P. schuppi* is distinguished by petiole shape (see above and compare Figs. 7 and 8) and differences in relative eye length (compare REL2).

Biology.— I have no field experience with this species and the museum material which I have examined contains no biological information. Luederwaldt (1926)

recorded *P. schuppi* nesting under epiphytes.

Material examined (BMNH, ICCM, LACM, MCSN, MCZC, MHNG, MZSP, NHMB, NHMV, PSWC, UCDC, USNM, WWBC).—

ARGENTINA *Misiones*: Iguazi (N. Kusnezov).

BRAZIL *AC*: Uranduique, Rio Branco (Machado & Pereira); *BA*: "Bahia" (c.u.); Encruzilhada, 960 m (Seabra & Alvarenga); Encruzilhada, 980 m (Seabra & Alvarenga); *DF*: Parque Nac. da Brasilia (W. L. & D. E. Brown); *ES*: Vila Velha (O. Seifert); *MG*: B. Horizonte (O. Monte); Juiz de Fora (Sampaio); Monsenhor Paulo (V. dos Santos); Passo Quarto (Sampaio); Pedra Azul, 800 m (Seabra & Alvarenga); S. Caraça (Engenho), 800 m (Martins & Silva); Tiradentes (R. L. Araujo); Três Coraçoes (E. Azcanjo); *MG?*: Tejuca (c.u.); *PR*: Col. Esperança, Arapongas (W. W. Kempf); Rolandia (W. W. Kempf); *RJ*: "Prov.Rio" (Göldi); "Rio Janeiro" (c.u.); Corcovado (Alvarenga & Seabra; c.u.); Fonseca, Niterói (C. R. Gonçalves); Ilha Jaguanum (D. Hunt); Ilha da Gipoia, Angra dos Reis (T. Borgmeier); Monumento Rodoviário (C. R. Gonçalves); Monumento Rodoviário, Via Dutra (C. R. Gonçalves); Petrópolis (c.u.); Tôco Sêco (R. L. Araujo); *RS*: "Rio Gr. do Sul" (Schupp); Laurentino (R. Müller); Pareci Novo (Hansen); São Leopoldo (Schupp); *SC*: Blumenau (R. L. Araujo; R. Müller; Reichensperger); Florianópolis (R. Müller); Gaspar (S. Fontes; R. Müller); Hamônia (Leuderwaldt); Itajaí (S. Fontes); Nova Teutônia (F. Plaumann); Poco Grande, Gaspar (R. Müller); Queçaba (T. Zimmermann); Rodeio (R. Müller); *SP*: "Mogy" (c.u.); Agudos (W. W. Kempf; R. Müller); Anhembi, Faz. Barr. Rico (W. W. Kempf *et al.*; L. Travassos F.); Atibaia (W. W. Benson); Barueri (K. Lenko); Botucatu (Göldi); Campo Limpo (W. W. Kempf); Caraguatatuba (Res. Flor.), 40 m (Exp. Depto. Zool.); Caraguatatuba (Res. Flor.), 680 m (K. Lenko); Embu (F. Lane); Est. Biol. Boraceia, Salesópolis (K. Lenko); Faz. Itaquerê, Bôa Esperança do Sul (K. Lenko); Faz. Itaquerê, Nova Europa (K. Lenko); Faz. Itaquerê, Tabatinga (K. Lenko); Guaratinguetá (W. W. Kempf); H. Florestal, S. Paulo (F. C. Val); Ilha do Cardoso (L. Foneris); Lençois Pta. (R. Müller); Rio Claro, Horto Florestal (V. Gama); Rio Manso (c.u.); Rodov-Ctba, km. 40 (W. W. Kempf); S. Rogue (F. Lane); S. Sebastião (W. W. Kempf); S. Sebastião, Bairro S. Francisco (W. W. Kempf); São Paulo (Parker); Ubatuba (P. C. Montouchet).

PARAGUAY Asunción (P. Duelli); Pastoreo (P. Duelli); San Bernardino (Fiebrig).

Pseudomyrmex urbanus (F. Smith)
(Figures 12a, 12b, 28, 29, 30)

Pseudomyrma urbana F. Smith 1877:65. Syntype workers, Ega, Amazonas, Brazil (BMNH) [Examined]; one worker here designated as LECTOTYPE.

Pseudomyrma chodati Forel 1920:201. Syntype workers, Paraguay (Chodat) (MHNG) [Examined]. One worker here designated LECTOTYPE. *Syn. nov.*

Pseudomyrma ogloblini Santschi, 1936:402. Syntype workers, Loreto, Misiones, Argentina (A. Ogloblin) (MCZC, MZSP, NHMB) [Examined]. *Syn. nov.*

Worker measurements (n=21).— HL 0.76–0.95, HW 0.58–0.66, MFC 0.014–0.026, CI 0.69–0.76, OI 0.52–0.58, REL 0.51–0.56, REL2 0.69–0.78, OOI 0.29–1.12, VI 0.76–0.85, FCI 0.022–0.041, SI 0.44–0.48, SI2 0.58–0.67, FI 0.44–0.53, PDI 1.08–1.53, MPI 0.028–0.063, NI 0.51–0.65, PLI 0.76–0.88, PWI 0.55–0.71, PPWI 1.06–1.48.

Worker diagnosis.— A relatively small species (HW 0.58–0.66), with moderately elongate eyes (REL2 0.69–0.78); sides of head (Fig. 12a) subparallel to broadly convex, rounding somewhat gradually into the flat to weakly concave occipital margin; second and third funicular segments broader than long (FLI 1.15–1.58, n=7). Fore femur relatively broad; metanotal groove well marked; basal face of propodeum subequal to, or longer than, the declivitous face and usually rounding gently into the latter. Petiole (Fig. 12b) longer than high, with soft dorsolateral margination, and a conspicuous anteroventral process; postpetiole broader than long. Mandibles striato–punctate; head densely punctate, sublucid, the punctures often separated by shiny interspaces, especially between the ocelli and compound eye, and immediately posterior to the compound eye, where some punctures are separated by half their diameters or more. Mesosoma punctate to coriarious-imbricate, tending to be sublucid dorsally and on the side of the pronotum, more opaque elsewhere. Petiole, postpetiole, and gaster sublucid, the lustre dulled by numerous fine piligerous punctures. Fine erect pilosity and appressed pubescence present on most of body, including mesosoma dorsum. Body usually light to medium orange-brown, with varying degrees of infuscation of the gaster,

hindfemur, and (sometimes) head; mandibles and tarsi paler. In a few individuals (Dpto. Beni, Bolivia; Isla Fernando Noronha, Brazil) entire body darker brown.

Comments.— *P. urbanus* belongs to a difficult species complex that also includes *P. caeciliae* and *P. cubaensis* (*s.l.*). *P. urbanus* workers are characterized by a combination of intermediate size (HW 0.58–0.66), relatively long eyes and broad fore femur (see Figs. 28, 29), and (typically) orange-brown body. These differences are detailed in the keys and in the discussions under *P. caeciliae* and *P. cubaensis*. *P. urbanus* differs from *P. elongatus* (*cf.* Figs. 6 and 12a) by its shinier appearance, particularly the presence of conspicuous sublucid areas on the head and pronotum, and by its lighter color. The eyes of *P. urbanus* workers tend to be shorter than those of *P. elongatus*, and the petiole is relatively lower.

Some problematic series are in the material listed below. These include unusually dark brown workers from Dpto. Beni, Bolivia and large *cubaensis*–like workers from Ecuador (Piedrero) and Venezuela (Edo. Zulia). The type specimens of *P. chodati* (Forel) and *P. ogloblini* (Santschi) from Paraguay and Argentina, respectively, appear to be rather typical *P. urbanus* insofar as they are in the appropriate size range (HW 0.58–0.61) and have a light orange-brown, sublucid integument; the eyes, however, are rather short (REL2 0.69–0.72). Future studies may reveal more than one species here.

Biology.— Little biological information is available about *P. urbanus*. Collections come from rain forest localities as well as areas typified by drier forest. The type series of *P. chodati* was collected in cauline swellings of *Cordia longituba*, that of *P. ogloblini* in the branches of "*Thecoma ipé*" [= *Tecoma obtusata*] accompanied by coccids; both records suggest a propensity for this species to nest in live plant cavities.

Material examined (BMNH, CKIC, CUIC, GHPC, JTLC, KWJC, LACM, MCZC, MHNG, MZSP, NHMB, PSWC, UCDC, USNM).—

ARGENTINA *Misiones*: Loreto (A. A. Ogloblin); Salta: Urundel (c.u.); *Tucumán*: Tucumán (W. Weyrauch).

BOLIVIA *Beni*: 46 km SSW San Borja, 300 m (P. S. Ward); *La Paz*: Espia Rio Bopi (W. M. Mann).

BRAZIL *AM*: Ega (Bates?); *FN*: Ilha Fernando Noronha (O. Roppa); *GO*: Anapolis (W. W. Kempf); Jatai (F. M. Oliveira); *MA*: Ilha de Balsas reg. (Westminster School Exp.); *MG*: Pedra Azul (Seabra & Alvarenga); Pirapora (E. Garbe); Varginha (Macais); *MS*: Corumba (D. Hunt); Faz. Canàa, Três Lagoas (F. Lane); *MT*: Sinop (M. Alvarenga); Utiariti, Rio Papagaio, 325 m (K. Lenko); Vila Vera (M. Alvarenga); *PA*: C. Araguaía (J. A. Rafael); Rio Trepecurú (Sampaio); *RD*: Vilhena (M. Alvarenga); *SP*: Agudos (C. Gilbert; W. W. Kempf); Faz. Itaquerê, Bôa Esperança do Sul (K. Lenko); Piracicaba (C. A. Triplehorn).

COLOMBIA *Guajira*: Serr. de Macuira, 6–8 km S Nazareth, 70–200 m (W. L. Brown & C. Kugler); *Meta*: R. Guayabero, Angostura 1, 270 m (C. Kugler); *Vichada*: Rio Tomo (W. W. Lamar).

ECUADOR *Pichincha*: Sto. Domingo (S. & J. Peck); *prov. unknown*: Piedrero (M. Deyrup).

FRENCH GUIANA 50 km S Cayenne (G. H. Perrault).

GUYANA *Rupununi*: Karanambo, 100 m (J. T. Longino).

PANAMA *Canal Zone*: Summit (N. H. L. Krauss); *Chiriqui*: "Prov.Chiriqui" (F. M. Gaige).

PARAGUAY: "Paraguay" (Chodat); Pastoreo (P. Duelli).

PERU *Loreto*: 15 km WSW Yurimaguas, 200 m (P. S. Ward); *Madre de Dios*: 30 km SW Pto. Maldonado, 290 m (T. L. Erwin *et al.*).

SURINAM Moengo, Cottica R. (c.u.); Paramaribo (c.u.).

TRINIDAD Curepe (F. D. Bennett); Maracas Valley (N. A. Weber).

VENEZUELA *Aragua*: 2 km N Ocumare de la Costa (A. S. Menke & L. Hollenberg); *Bolívar*: Campamento Rio Grande, 250 m (P. S. Ward); *T. F. Amazonas*: P. N. Duida–Marahuaka, Culebra, 250 m (K. Jaffé); *T. F. Delta Amacuro?*: "Orinoco Delta" (N. A. Weber); *Zulia*: El Tucuco, Perija (R. W. Brooks *et al.*).

PSEUDOMYRMEX SUBTILISSIMUS GROUP

Introduction

Diagnosis (worker).— Small species (HW 0.48–0.73), with subopaque, densely punctulate, and elongate head (CI 0.56–0.73); mandibles as in the *P. oculatus* group; frontal carinae distinctive: subcontiguous (FCI 0.023–0.066), raised anterodorsally, and merging insensibly into the clypeus (rather than fusing with the antennal sclerite) (Fig. 18), so that in lateral view they form a continuous curve with the median clypeal lobe (Fig. 19); the latter tectiform and protruding, with the anterior margin weakly flared and sharp-edged laterally, but not medially; in dorsal view, median clypeal lobe broadly rounded anteriorly; scapes very short (SI2 0.44–0.59); funicular segments II and III much broader than long (FLI 0.96–1.30); fore femur notably broadened (FI 0.44–0.60); petiole relatively low, long, and slender (PLI 0.54–0.75, PWI 0.48–0.68), without a differentiated peduncle and node, appearing dorsally flattened in lateral profile. Erect pilosity very sparse, lacking on the antennae, legs, and most of head and mesosoma; a characteristic pair of rather long setae present on the pronotal humeri, on the propodeum at the juncture of the basal and declivitous faces, and on the petiolar dorsum. Pubescence covering most of the body, exceptionally fine and inconspicuous in three of the four species. Palp formula: 6,3.

Comments.— This is a small, discrete group of species, uniquely characterized by the configuration of the frontal carinae and the clypeus. The elongate head, short scapes, flattened apedunculate petiole, and patterns of pilosity are also distinctive.

Features shared with the *P. oculatus* group include the protruding, tectiform, median clypeal lobe; palp formula of 6, 3; and elongate head and eyes. In addition preliminary observations suggest similarities in the male genitalia which, together with the shared worker characters, support the notion of a close relationship between these two groups.

Synonymic List of Species

P. spiculus, sp. nov. Mexico to Peru, Bolivia

P. subtilissimus (Emery, 1890). Nicaragua, Costa Rica

P. tenuissimus (Emery, 1906), *stat. nov.* Mexico to Peru, Brazil
    = *P. culmicola* (Forel, 1912), syn. nov.

P. villosus, sp. nov. Brazil

Key to Species (workers and queens)

Note.— Only a few queens have been examined (unknown in *P. villosus*) and the ranges of measurements and indices for queens may be somewhat broader than the known limits given here.

1   Small species (HW < 0.67) with elongate head and eyes (worker CI 0.56–0.71, queen CI 0.43–0.61; worker REL2 0.76–0.92, queen REL2 0.84–1.15) (Figs. 32, 34, 36); pubescence very short and inconspicuous, tightly appressed to body 2

1'   Larger species (HW 0.73, in unique worker type), with relatively broad head and short eyes (CI 0.73, REL2 0.72) (Fig. 38); body pubescence conspicuous, decumbent to suberect (Brazil)... *P. villosus, sp. nov.*, p. 434

2   (1)   Very small species (worker HW 0.48–0.53; queen HW 0.42–0.51, n=5), with elongate head (worker CI 0.56–0.62; queen CI 0.43–0.53) and slender petiole (worker PLI 0.54–0.66; queen PLI 0.55–0.62) (Figs. 36, 37) (Mexico to Peru, Brazil)................................*P. tenuissimus* (Emery), p. 432

2'   Larger species (worker HW 0.55–0.66; queen HW 0.56–0.63, n=6), with broader head (worker CI 0.60–0.71; queen CI 0.55–0.61); if worker HW < 0.60, then petiole generally rather short (worker PLI 0.65–0.75) 3

3   (2')   Smaller species (worker HW 0.55–0.59; queen HW 0.56, 0.57, n=2) with more elongate head (worker CI 0.60–0.65, queen CI 0.55, 0.57) and with relatively short petiole (worker PLI 0.65–0.75, queen PLI 0.63, 0.68) (Figs. 34, 35) (Nicaragua, Costa Rica)................................*P. subtilissimus* (Emery), p. 432

3'   Larger species (worker HW 0.61–0.66; queen HW 0.61–0.63, n=4), with broader head (worker CI 0.66–0.71; queen CI 0.60–0.61) and slender petiole (worker PLI 0.56–0.67; queen PLI 0.56–0.61) (Figs. 32, 33) (Mexico to Peru, Brazil) ....
           .... *P. spiculus, sp. nov.*, p. 431

Species Accounts

Pseudomyrmex spiculus sp. nov.
(Figures 31, 32, 33)

Pseudomyrmex subtilissimus tenuissimus; Kempf (nec Emery) 1972:224 (partim).

Holotype Worker.— COSTA RICA, *Prov. Puntarenas*: Reserva Biologica Carara, 500m, 9°47'N, 84°36'W, 26.viii.1985, on low vegetation, old field/pasture,

P. S. Ward acc. no. 7668–9 (MCZC). HW 0.63, HL 0.89, EL 0.50, PL 0.37, PH 0.22.

Paratype Workers, Queens.— Same data as holotype, two workers; COSTA RICA, *Prov. Puntarenas*: Manuel Antonio Natl. Park, 10m, 9°23'N, 84°09'W, 28.vii.1985, P. S. Ward acc. no. 7715–6, 1 worker; same locality, 40m, 27.vii.1985, P. S. Ward acc. no. 7679, 1 dealate queen; Llorona, Corcovado Natl. Park, 10m, 10–14.v.1979, P. S. Ward acc. no. 3389–6, 1 worker; Sirena, Corcovado Natl. Park, 50m, 8°28'N, 83°35'W, 22.iv.1981, J. T. Longino, 1 worker; same locality, 20.xii.1981, J. T. Longino, 1 worker; COSTA RICA, *Prov. Limón*: Portete, 13.ii.1965, D. H. Janzen, 1 worker. (JTLC, LACM, MNCR, MZSP, PSWC, USNM).

Type series is restricted to the above material from Costa Rica. Additional, apparently conspecific material comes from Mexico, Panama, Colombia, Guyana, Brazil, and Peru (see "Material examined" below).

Worker measurements (n=14).— HL 0.88–0.98, HW 0.61–0.66, MFC 0.022–0.042, CI 0.66–0.71, OI 0.55–0.61, REL 0.53–0.57, REL2 0.76–0.83, OOI 0.04–0.67, VI 0.79–0.87, FCI 0.034–0.064, SI 0.38–0.43, SI2 0.46–0.54, FI 0.48–0.55, PDI 1.20–1.61, MPI 0.029–0.059, NI 0.60–0.71, PLI 0.56–0.67, PWI 0.48–0.59, PPWI 1.14–1.37.

Worker diagnosis.— Small, slender species (HW 0.61 – 0.66); head (Fig. 32) elongate, although broader than that of *P. tenuissimus* (CI 0.66–0.71); eyes elongate, almost reaching the level of the median ocellus; occipital margin concave in full face, dorsal view; lateral margins of pronotum rounded; fore femur short and broad (FI 0.48–0.55); metanotal groove narrow, shallow; basal face of propodeum convex, declivitous face flat to weakly concave, the former about 1.5 times the length of the latter; basal face of propodeum rounding into the declivitous face at a slight (obtuse) angle, marked by a pair of erect setae; petiole (Fig. 33) slender, low, notably longer than wide (Fig. 31; PLI 0.56–0.67); postpetiole short, globose in lateral view, subtriangular in dorsal view, about as wide as long, and twice as wide as the petiole (PWI2 0.51–0.57). Mandibles finely striate with scattered punctures, sublucid; head, mesosoma, and petiole densely punctulate to coriarious-imbricate, opaque; postpetiole and gaster opaque, with numerous fine piligerous punctures. Erect pilosity very sparse (except on apex of gaster), lacking on the antennae, sides of head, upper half of gula, femora (except for one to several setae on the ventral surface of the fore femur), tibiae, tarsi, and most of mesosoma. Two or three pairs of short erect setae on dorsum of head; a conspicuous pair of long (ca. 0.15 mm) erect setae on the anterolateral corners of pronotum, at the juncture of the basal and declivitous faces of the propodeum, and on the posterior dorsum of both the petiole and postpetiole; the last two pairs often accompanied by a pair of shorter, posterolateral setae. Appressed pubescence common on most of body, but rather fine and inconspicuous. Grey-brown; mandibles, fronto-clypeal complex, antennae, tarsi, pronotum, petiole, and postpetiole paler luteous-brown.

Comments.— The combination of relatively large size, broad head, and slender petiole serves to distinguish *P. spiculus* from the other species in the *P. subtilissimus* group (see Figs. 31–39).

Biology.— The species is widespread but infrequently collected, and little is known about its biology. Most collections are based on single individuals foraging on low vegetation or tree-falls, in rain forest, rain forest edge, littoral forest, and mangrove. In Costa Rica I collected a single dealate (colony-founding?) female in a loose dead twig, hanging in low vegetation, in coastal rain forest. Type workers from Reserva Biologica Carara were foraging on the trunk and associated vegetation of a strangler fig tree (*Ficus oerstediana*) and its unidentified host tree, in an old pasture. At this location, workers of *P. tenuissimus* were present on the same

vegetation, foraging in close proximity to those of *P. spiculus*. These two species have been collected sympatrically elsewhere, and their ranges are broadly coextensive.

Material examined.— Type material listed above, plus the following (INPA, LACM, MCZC, MZSP, PSWC, UCDC):

BRAZIL *AM*: Manaus to Itacoatiara Hwy., km 34 (W. L. & D. E. Brown), *MT*: Sinop 55°37'W, 12°31'S (M. Alvarenga); *RD*: Vilhena (A. Y. Harada).

COLOMBIA *Magdalena*: 4km N San Pedro, 550m (P. S. Ward); Cañaveral, < 5m (P. S. Ward).

GUYANA *Mazaruni-Potaro*: Kartabo (W. M. Wheeler); *Rupununi*: Upper Essequibo (J. G. Myers).

MEXICO *Jal.*: 14 km SSE Chamela, 20 m (P. S. Ward).

PANAMA *Canal Zone*: 5 km WNW Gatun Dam, 160 m (P. S. Ward); Barro Colorado I. (N. Banks; R. B. & L. S. Kimsey); *Colón*: Colón (E. Adams).

PERU *Madre de Dios*: Rio Tambopata Reserve, 30km SW Pto. Maldonado, 290m (T. L. Erwin *et al.*).

Pseudomyrmex subtilissimus (Emery)
(Figures 31, 34, 35)

Pseudomyrma subtilissima Emery 1890:65. Syntype workers, one dealate queen, Alajuela, Costa Rica (Alfaro) (MCSN) [Examined]. One syntype worker here designated as LECTOTYPE.

Worker measurements (n=17, except for FI where n=16).— HL 0.86–0.95, HW 0.55–0.59, MFC 0.020–0.032, CI 0.60–0.65, OI 0.52–0.59, REL 0.49–0.54, REL2 0.80–0.87, OOI 0.38–0.89, VI 0.79–0.88, FCI 0.035–0.055, SI 0.41–0.47, SI2 0.50–0.57, FI 0.44–0.53, PDI 1.60–1.88, MPI 0.015–0.039, NI 0.52–0.66, PLI 0.65–0.75, PWI 0.56–0.68, PPWI 1.18–1.35.

Worker diagnosis.— Similar to *P. spiculus* (*q.v.*) except as follows: smaller, head (Fig. 34) more elongate (HW 0.55–0.59, CI 0.60–0.65), eyes shorter, not reaching the level of the median ocellus (REL 0.49–0.54); basal face of propodeum flatter, meeting the declivitous face at a more distinct angle; petiole (Fig. 35) shorter, higher (PLI 0.65–0.75). Most of body uniformly light brown; gaster dark brown, with contrasting light brown band on anterior half of abdominal tergite IV.

Comments.— A moderately elongate head (broader than *P. tenuissimus*, more elongate than *P. spiculus* and *P. villosus*; see Fig. 31), short petiole, and light brown color (with banded gaster) characterize *P. subtilissimus*.

Biology.— This species has been collected only in, or on, swollen-thorn acacias, in association with *Pseudomyrmex flavicornis* (F. Smith). The collection records suggest that it is an obligate, non–aggressive acacia ant which somehow manages to coexist with *P. flavicornis*.

Material examined (BMNH, LACM, MCSN, MHNG, MZSP, NHMV, PSWC, USNM).—

COSTA RICA *Alajuela*: Alajuela (Alfaro); *Puntarenas*: 1km NE Tárcoles, 20m (P. S. Ward); Est. Biol. Palo Verde, 10 m (J. T. Longino); *San José*: 3.5km NE Santiago de Pur (D. H. Janzen); Rio Oro (D. H. Janzen); *prov. unknown*: "Costa Rica" (Alfaro; Cameron; c.u.).

NICARAGUA *Matagalpa*: 15.8 mi. W Jebaca [= Sebaco] (D. H. Janzen).

Pseudomyrmex tenuissimus (Emery) *stat. nov.*
(Figures 18, 19, 31, 36, 37)

Pseudomyrma subtilissima subsp. *tenuissima* Emery, 1906:119. Holotype (unique syntype) worker, Corumba, Matto Grosso [do Sul], Brazil, 15.viii.1900, (MCSN) [Examined].
Pseudomyrma culmicola Forel, 1912:217. Holotype (unique syntype) worker, Trinidad (Forel) (MHNG)

[Examined]. *Syn. nov.*
Pseudomyrmex subtilissimus; Wheeler & Wheeler (nec Emery), 1973:207 [description of larva].

Worker measurements (n=30, except for FI where n=29).— HL 0.82–0.93, HW 0.48–0.53, MFC 0.011–0.033, CI 0.56–0.62, OI 0.50–0.58, REL 0.48–0.53, REL2 0.84–0.92, OOI 0.22–0.89, VI 0.85–0.90, FCI 0.023–0.066, SI 0.39–0.46, SI2 0.44–0.54, FI 0.52–0.60, PDI 1.58–2.14, MPI 0.022–0.055, NI 0.55–0.64, PLI 0.54–0.66, PWI 0.49–0.60, PPWI 1.05–1.34.

Worker diagnosis.— Similar to *P. spiculus* (*q.v.*) except as follows: distinctly smaller, head (Fig. 36) more elongate (HW 0.48–0.53, CI 0.56–0.62). Basal face of propodeum flatter, forming a more distinct angle with the declivitous face. Body color more uniformly brown to grey–brown, the pronotum, petiole, and postpetiole only slightly, or not at all, contrastingly lighter.

Comments.— *P. tenuissimus* can be distinguished from *P. subtilissimus* by its darker color, smaller size, and longer petiole (compare Figs. 35 and 37). It differs from *P. spiculus* by its smaller size and more elongate head (compare HW and CI; see Fig. 31). The unique syntype (holotype) of *P. culmicola* fits easily within this concept of *P. tenuissimus*.

Biology.— Although *P. tenuissimus* is the most common member of the *P. subtilissimus* group, most collections appear to based on scattered foragers. In Costa Rica, Panama, and Colombia, I have encountered workers foraging on vegetation in a variety of habitats including rain forest, rain forest edge, old field/pasture, and tropical dry forest. I have seen nests only twice: one was a small colony containing a single dealate queen, seven workers, and brood, in the dead, fibrous twig of a woody liana, in tropical dry forest (northern Colombia); the other was a nest of 13 workers, 16 alate queens, and brood in the dead twig of a thorny vine at the edge of disturbed second–growth rain forest (Edo. Barinas, Venezuela). Mann (1916:426) recorded a colony from Maranhao, Brazil "taken from beneath a loose piece of bark", an unusual nest-site for *Pseudomyrmex* as Mann himself remarks.

Material examined (INPA, IZAV, JTLC, KWJC, LACM, MCSN, MCZC, MHNG, MZSP, PSWC, UCDC, USNM, WPMC, WWBC).—

BELIZE Belize (N. L. H. Krauss).

BOLIVIA *Beni*: Cavinas (W. L. Mann).

BRAZIL *AM*: Faz. Esteio, 80 km NNE Manaus, 80 m (P. S. Ward); Manaus, 60 m (P. S. Ward); Rio Tarumá Mirim-Igapó (J. Adis); Tarumá-Mirim (J. Adis); km. 27, ZF–3, near Manaus (W. W. Benson); *CE*: Itapipoca (C. R. Gonçalves); *ES*: Vitória, Penha (R. Müller); *GO*: Jatai (F. M. Oliveira); *MA*: "Maranhao" (W. M. Mann; c.u.); Bacabal (W. W. Kempf); *MG*: Pedra Azul (F. M. Oliviera); Arassuahy (Thieman); *MS*: Corumbá (c.u.); Imbirussú-Corumbá (K. Lenko); *MT*: Sinop (M. Alvarenga); Utiariti, Rio Papagaio, 325m (K. Lenko); Vila Vera (M. Alvarenga); *PA*: Belém (C. R. Gonçalves); C. Araguaia (J. A. Rafael; A. Y. Harada); Igarapé-Açu (C. R. Gonçalves); S. Norte, Carajás (W. W. Benson); *RJ*: Fonseca, Niterói (C. R. Gonçalves); *RN*: Natal (W. M. Mann); *SP*: Faz. Campininha, Mogi Guaçu (H.C.M.).

COLOMBIA *Caquetá*: Florencia (W. P. MacKay); *Cundinamarca*: El Colegio & Anapoima (I. Zenner); *Huila*: 15 mi. S Neiva (W. & E. MacKay); 15 mi. W Campoalegre (W. & E. MacKay); Colombia (W. & E. MacKay). *Magdalena*: 8km NE Cienaga, 40m (P. S. Ward); Cañaveral, 50m (P. S. Ward); *Magdalena?*: locality illegible (A. Forel); *Meta*: Carimagua (M. Corn); *Valle*: Dagua (W. & E. MacKay).

COSTA RICA *Alajuela*: 11 mi. N. Florencia (D. H. Janzen); *Heredia*: F. LaSelva, 3km S Pto. Viejo (H. A. Hespenheide); 3 km S Pto. Viejo (J. T. Longino); *Limón*: Portete (D. H. Janzen); *Puntarenas*: Boca Barranca (D. H. Janzen); Llorona, Corcovado Natl. Park, 0–100m (J. T. Longino); Llorona, Corcovado Natl. Park, 10m (P. S. Ward); Reserva Biol. Carara, 500m (P. S. Ward); Sirena, Corcovado Natl. Park, 0–100m, 50m (J. T. Longino).

ECUADOR *prov. unknown*: Piedrero (M. Deyrup).

EL SALVADOR *San Salvador*: Lago de Ilopango, N. side (R. Silberglied).

FRENCH GUIANA Cayenne (Pillault).

GUYANA *East Demerara-West Coast Berbice*: Botanic Gardens, Georgetown (H. Morrison); *Mazaruni-Potaro*: Kartabo (W. M. Wheeler).

HONDURAS *Cortes*: Lago Yojoa, 680m (W. L. Brown).

JAMAICA Kingston (N. L. H. Krauss); *St. James*: Great R., 0–80m (J. T. Longino); *Trelawny*: Green Park, 0–150m (J. T. Longino).

MEXICO *Oax.*: 5 mi. E Temascal (D. H. Janzen); *S.L.P.*: Tamazunchale (W. S. Ross); *Ver.*: Pueblo Nuevo, nr. Tetzonapa (E. O. Wilson); Rio Tonto (D. H. Janzen); 29.5 mi. NW Tuxpam on Hwy. 122 (D. H. Janzen).

NICARAGUA *Matagalpa*: El Tuma, 30km E Matagalpa, Hwy. 5, 330m (C. Kugler & J. Hahn).

PANAMA *Canal Zone*: 3km SW Gatun, 100m (W. L. Brown *et al.*); 5km WNW Gatun Dam, 160m (P. S. Ward); Barro Colorado I. (W. M. Wheeler; H. Wolda); Cerro Galera, 9km W Panama City (W. L. Brown *et al.*); Mt. Hope, nr. Colon (W. M. Wheeler); Ruta 1, 14km W Panama City, 100m (Brown, W. L. *et al.*); *Panamá*: Chilibra R. (W. M. Wheeler); Rio Piedras (D. H. Janzen); Taboga Island (A. Busck); *prov. unknown*: Lilina R. (W. M. Wheeler).

PERU *Huánuco*: Panguana, 200 m (M. Verhaagh); *Junín:* Valle Chanchamayo, 800 m (Weyrauch); *dpto. unknown*: Queb. Penaga, Anotape Mts. (Frizzell)

TRINIDAD Curepe (F. D. Bennett); Mayaro Bay (N. Weber); St. Augustine (N. Weber; Darlington); "Trinidad" (Forel).

VENEZUELA *Apure*: Mantecal (H. Romero); *Barinas*: 10km WNW Santa Barbara, 280 m (P. S. Ward); 17 km SSW Ciudad Bolivia, 240 m (P. S. Ward); Rio Capara Res. Stn., 32 km E El Canton (J. B. Heppner); *Carabobo*: Hda. El Palmar, Las Trincheras, 850m (J. & B. Bechyne); *T. F. Delta Amacuro?*: "Orinoco Delta" (N. A. Weber); *Zulia*: El Tucuco, Perija (R. W. Brooks *et al.*).

Pseudomyrmex villosus sp. nov.
(Figures 38, 39)

Holotype Worker.— BRAZIL, *MT*: Utiariti, Rio Papagaio [= Rio Sauêruiná] [13°02'S, 58°17'W], 325m, viii.1961, K. Lenko (MZSP).

Holotype measurements.— HL 1.00, HW 0.73, MFC 0.038, EL 0.53, PL 0.38, PH 0.27, CI 0.73, OI 0.60, REL 0.53, REL2 0.72, OOI 0.51, VI 0.81, FCI 0.052, SI 0.43, SI2 0.59, FI 0.50, PDI 1.50, MPI 0.035, NI 0.62, PLI 0.71, PWI 0.64, PPWI 1.39.

Worker diagnosis.— A large species (for the *P. subtilissimus* group) with broad head and relatively short eyes (Fig. 38). Sides of head broadly convex, rounding into the distinctly concave occipital margin. Fore femur broad; metanotal groove rather shallow; basal face of propodeum slightly convex (lateral view), rounding into the much shorter declivitous face. Petiole (Fig. 39) relatively short and high, with a distinct anteroventral tooth; postpetiole broader than long.

Mandibles striato-punctate, subopaque. Head densely punctulate, sublucid, with shiny interspaces between the fine, partially effaced punctulae. Remainder of body punctulate to coriarious-imbricate, largely sublucid. Erect pilosity sparse, distributed as in *P. spiculus* (*q.v.*). Pubescence common on most of body, many hairs decumbent to suberect, and thus more conspicuous than in other members of the *P. subtilissimus* group. Body brown, mandibles, tarsi, petiole, postpetiole, and (to a lesser extent) pronotum and antennae lighter (luteous-brown) in color.

Comments.— Known only from the holotype worker, this species can be recognized by its large size, broad head, short eyes, and rather conspicuous (subdecumbent) pubescence. The short petiole and sublucid integument are also distinctive.

TAXONOMIC COMMENTS ON OTHER *PSEUDOMYRMEX* SPECIES
Introduction

The following notes are based on critical examination of type material in various (mostly European) collections, supplemented by infusions of fresh material from recent field work in Central and South America. Most of the new synonymies given here are those that I consider relatively clear and straightforward. Much additional synonymy is certain, but this cannot be documented reliably without detailed species-level revisions of the groups concerned. Despite such synonymy, it should also be pointed out that there are considerable numbers of undescribed species, especially in the *P. pallidus* group.

Twenty-two species and 64 available names are formally dealt with below. The valid species are listed alphabetically and described briefly, with related taxa discussed or cross-referenced where appropriate. I have given particular attention to species associated with ant-plants (*Acacia, Tachigali, Triplaris, etc.*) because these have received considerable ecological attention, often accompanied by taxonomic inaccuracies. Grouped according to the plants which they inhabit, the following plant-associated species of ants are discussed and diagnosed:

Acacia   *P. ferrugineus, P. flavicornis, P. nigrocinctus* (under *P. ferrugineus*), *P. nigropilosus* (under *P. ferrugineus*), *P. spinicola, P. subtilissimus* (above, p. 432). See also note added in proof on *P. peperi* (p. 452).

Pithecellobium

             P. perboscii

Tachigali *P. concolor, P. malignus, P. tachigaliae*

Triplaris *P. dendroicus, P. triplaridis, P. triplarinus* (under *P. dendroicus*), *P. viduus*

P. viduus occurs in association with additional ant-plant genera (*Ocotea, Cordia, Sapium, etc.*), displaying a catholicity not found in the other *Pseudomyrmex.*

Species accounts

Pseudomyrmex concolor (F. Smith)
(Figure 40)

Pseudomyrma concolor F. Smith, 1860:70. Syntype dealate queen (unique?), "St. Paul" [São Paulo de Olivença], Amazonas, Brazil (BMNH) [Examined].

Pseudomyrma penetrator F. Smith, 1877:66. Syntype alate queen, "St. Paul" [São Paulo de Olivença], Amazonas, Brazil (BMNH) [Examined] [Synonymy by Kempf, 1967:5; here confirmed].

Pseudomyrma latinoda Mayr, 1877:877. Holotype worker, Amazonas [probably Barreiras de Unahan, Rio Purus; see Benson & Setz, 1985], Brazil (Trail) (NHMV) [Examined]. *Syn. nov.*

Pseudomyrma damnosa Wheeler, 1921b:139. Syntype workers, queens, males, Kartabo, Guyana (W. M. Wheeler) and Penal Settlement, Guyana (W. M. Wheeler) (MCZC) [Examined] [Synonymy, under *P. latinodus* (Mayr), by Kempf, 1961:406; here confirmed].

This is a widespread *Tachigali*-inhabiting species, usually going by the name *P. latinodus* (Mayr). Comparison of the type queen of *P. concolor* with worker-associated queens of *P. latinodus* from Brazil, Guyana, and Venezuela, shows that the two are conspecific. Among the several species of *Pseudomyrmex* associated with *Tachigali*, the queens and workers of *P. concolor* are recognized by the following combination of features: upper third of the head predominantly smooth and shining, with scattered punctures of variable density; median clypeal lobe ventrally deflected and without lateral teeth or angles (Fig. 40); erect pilosity conspicuous on most parts of the body, including the sides of the head; light orange-brown in color.

The relationship of *P. concolor* to the four forms described as varieties of *P. latinodus*, namely *P. coronatus (Wheeler), P. endophytus* (Forel), *P. nigrescens* (Forel), and *P. opacior* (Forel), is unclear. Closely related but distinct species in this complex include *P. malignus* (Wheeler) (*q.v.*) and *P. tachigaliae* (Forel) (*q.v.*), differing in pilosity and clypeal configuration (compare Figs. 40, 41, 42).

Pseudomyrmex dendroicus (Forel), *stat. reval.*

Pseudomyrma dendroica Forel, 1904a:40. Syntype workers, males, Rio Purus, Amazonas, Brazil (A. Göldi) (MCSN, MHNG, MZSP) [Examined]. One syntype worker in MHNG here designated LECTOTYPE. *Stat. reval.* [Incorrectly synonymized with *P. triplarinus* (Weddell) by Kempf, 1961:408]

Pseudomyrma dendroica var. *emarginata* Forel, 1904b:684. Syntype workers, queen, Mavany Jurua, Amazonas, Brazil (Ule) (MCSN, MHNG) [Examined] *Syn. nov.* [Incorrectly synonymized with *P. triplarinus* (Weddell) by Kempf, 1961:408]

This ant is one of several *Pseudomyrmex* species which are obligate inhabitants of trees of the genus *Triplaris*. Workers of *P. dendroicus* are distinguished from those of the closely related species, *P. triplarinus* (Weddell) (= *P. arborissanctae* (Emery)), by the following features: (i) more widely separated frontal carinae; (ii) dark brown head, contrasting with a lighter-colored mesosoma (head and mesosoma more or less concolorous in *P. triplarinus*); (iii) subpetiolar process usually subrectangular and recurved backwards to some degree (subtriangular in *P. triplarinus*); (iv) erect pilosity less abundant; fewer than 10 standing hairs in outline on outer surface of hind tibia (erect pilosity more conspicuous and abundant in *P. triplarinus*).

See also descriptions of *P. triplaridis* (Forel) and *P. viduus* (F. Smith).

Pseudomyrmex ejectus (F. Smith)

Pseudomyrma ejecta F. Smith, 1858:157. Lectotype worker, "Brazil?" (BMNH) [Examined] [Lectotype designation and discussion of type locality by Ward, 1985:231].

Ponera (Ectatoma) [sic] *lincecumii* Buckley, 1866:172. Syntype worker(s), "On trees in Central Texas" [type(s) lost; not examined]. *Syn. nov.*

In a recent review of the Nearctic species of *Pseudomyrmex* (Ward, 1985) I did not consider this long-standing *nomen dubium*. The original description supports

Smith's (1951,1958) placement of *Ponera lincecumii* in the Pseudomyrmecinae. Among the species of Pseudomyrmecinae occurring in central Texas, only *Pseudomyrmex ejectus* (F. Smith) conforms to Buckley's description with respect to size and color ("length 0.15 inch. Upper surface of head and abdomen sub-piceous, the rest reddish-yellow or pale yellow...") and there is nothing in Buckley's description which precludes *P. ejectus*. As the Nearctic *Pseudomyrmex* species are now relatively well-known (Ward, 1985), the synonymy seems reasonably secure.

Pseudomyrmex euryblemma (Forel)

Pseudomyrma euryblemma Forel, 1899:90. Syntype worker, (unique), Alajuela, Costa Rica (Alfaro) (MCSN) [Examined].

Pseudomyrma kurokii Forel, 1906:226. Syntype worker (unique), Sierra Nevada de Santa Marta, Colombia (Forel) (MHNG) [Examined]. *Syn. nov.*

P. euryblemma is a common and widespread species, whose laterally angulate median clypeal lobe (in workers and queens) and anteroventrally recurved pygidium (in males), clearly place it in the *P. pallidus* group. Workers of this species have a broad head (HW 0.81–0.98, CI 0.86–0.92; n=14) whose puncticulate-coriarious sculpture weakens towards the vertex (which is sublucid); wide but shallow metanotal groove; long basal face of the propodeum; and pubescent fourth abdominal tergite. The propodeal spiracles are rather salient in dorsal view, and individuals are typically dark brown in color.

See also *P. holmgreni* (Wheeler) and *P. rufiventris* (Forel).

Pseudomyrmex ferrugineus (F. Smith)
(Figure 45)

Pseudomyrma ferruginea F. Smith, 1877:64. Syntype workers, Mexico (BMNH) [Examined]; one worker here designated LECTOTYPE.

Pseudomyrma belti race *fulvescens* Emery, 1890:64. Syntype workers, Guatemala (Beccari) (MCSN) [Examined] *Syn. nov.* One worker here designated LECTOTYPE.

Pseudomyrma canescens Wasmann, 1915:321. Syntype workers, Tampico, Mexico (Brakhoven) (MCSN, MCZC) [Examined] *Syn. nov.* (Also preoccupied).

Pseudomyrma wasmanni Wheeler, 1921a:22. Replacement name, now unnecessary, for *P. canescens* Wasmann, 1915 (nec F. Smith, 1877).

Pseudomyrma belti subsp. *bequaerti* Wheeler, 1942:164. Syntype workers, Puerto Castillo, Honduras (J. Bequaert) (MCZC) [Examined] *Syn. nov.* One worker here designated LECTOTYPE.

Pseudomyrma belti subsp. *saffordi* Wheeler, 1942:162. Syntype workers, Chicoasen, Chiapas, Mexico (G. N. Collins) (MCZC) [Examined] *Syn. nov.* One worker here designated LECTOTYPE.

Pseudomyrma belti subsp. *vesana* Wheeler, 1942:163. Holotype (unique syntype) worker, Cordoba, Mexico (F. Knab) (MCZC) [Examined] *Syn. nov.*

Pseudomyrma belti subsp. *bequaerti* Enzmann, 1945:80. Syntype workers, Puerto Castillo, Honduras (J. Bequaert) (MCZC) [Examined] [Objective synonym of *P. belti bequaerti* Wheeler; Brown, 1949:42].

Pseudomyrma kuenckeli var. *hondurana* Enzmann, 1945:87. Three syntype workers, Honduras (Bates) (MCZC) [Examined]; one syntype here designated LECTOTYPE. *Syn. nov.* [Incorrectly synonymized under *P. kuenckeli* (Emery) by Kempf, 1961:402].

P. ferrugineus (F. Smith) is an obligate inhabitant of swollen-thorn acacias, distributed from Mexico to Honduras, whose interaction with the acacias was the

subject of a detailed experimental study by Janzen (1967). The worker of *P. ferrugineus* has a densely punctate head which is nevertheless weakly sublucid in the area between the ocelli and upper margin of the compound eye; the median clypeal lobe is anteroventrally subtended and without lateral angles or teeth (Fig. 45); and the body is variable in color, usually brown or dark brown, the mesosoma sometimes lighter in color than the head and gaster.

The Costa Rican acacia-ant reported in the ecological literature as "*Pseudomyrmex ferruginea*" (*e.g.,* Janzen, 1983) is, in fact, *P. spinicola* (Emery) (*q.v.*). The two other common members of the *P. ferrugineus* group in Costa Rica are *P. flavicornis* (F. Smith) (*q.v.*) and the small (worker HW < 0.85), orange-brown species, *P. nigrocinctus* (Emery). A fourth species of acacia-ant, *P. nigropilosus* (Emery), is a member of the *P. gracilis* group and is recognizable by its large size (worker HW > 1.16), elongate eyes which almost reach the level of the median ocellus, laterally submarginate pronotum, and conspicuous black pilosity (further description in Kempf, 1958). Like *P. subtilissimus* (see above, p. 432) *P. nigropilosus* is a non-aggressive species, whose workers provide no protection to the acacia that they occupy (Janzen, 1975).

Pseudomyrmex filiformis (Fabricius)

Formica filiformis Fabricius, 1804:405. Syntype dealate queen, Essequibo, Guyana (Smidt) (ZMUC) [Examined]; here designated as LECTOTYPE. A second syntype dealate queen in ZMUC, lacking head, metasoma, and a locality label, has been labelled paralectotype.

Pseudomyrma cephalica F. Smith, 1855:168. Dealate queen, labelled as type, Santarem, Brazil (Bates); two workers, probable syntypes, Villa Nova, Brazil (Bates) (BMNH) [Examined] [Synonymy by Roger, 1862:289].

Pseudomyrma biconvexa Forel, 1899:95. Syntype workers, Pantaleon, Guatemala (Champion) (BMNH, MHNG); Costa Rica (Tonduz) (BMNH) [Examined] [Synonymy by Wheeler, 1919:125].

Pseudomyrma biconvexa var. *longiceps* Forel, 1906:229. Syntype worker, Santa Marta, Colombia (A. Forel) (MHNG) [Examined]. *Syn. nov.*

Pseudomyrma longiceps Stitz, 1933:69. Holotype queen, Macuto, near La Guayra, Venezuela (C. Gazgo) (not in ZMUH, probably destroyed during World War II). *Syn. nov.* (Also preoccupied).

The syntype worker of *P. longiceps* (Forel) is simply a large *P. filiformis* worker, with a rather elongate head and a conspicuous subpetiolar tooth. I have seen such variant workers within nest-series of typical *P. filiformis* from elsewhere in Central and South America. Although the unique type of *P. longiceps* (Stitz) is lost, the original description (particularly as it pertains to head length, position of eyes, and petiole shape) is closer to that of *P. filiformis* than any other species known to me.

Pseudomyrmex flavicornis (F. Smith)

Pseudomyrma flavicornis F. Smith, 1877:67. Three syntype workers, Nicaragua (BMNH) [Examined]. One syntype here designated LECTOTYPE.

Pseudomyrma belti Emery, 1890:63. Syntype workers, queens, Alajuela, Costa Rica (MCSN) [Examined]. *Syn. nov.*

Pseudomyrma belti var. *obnubila* Menozzi, 1927:273. Syntype worker, San José, Costa Rica (H. Schmidt)

(NHMB) [Examined]. *Syn. nov.*

Pseudomyrma belti subsp. *fellosa* Wheeler, 1942:160. Syntype workers, Nicaragua (W. Fluck); Granada, Nicaragua (C. F. Baker) (MCZC) [Examined]. *Syn. nov.*

P. flavicornis is a widespread Central American acacia-ant, referred to in most publications as *P. belti*. Because the taxonomic status of *P. belti* and its various "subspecies" or "varieties" has never been fully clarified, I have little hesitation in replacing *P. belti* with the less well-known senior synonym. Of the various infraspecific names associated with *P. belti* (see Kempf, 1972), only two (*P. obnubilus* and *P. fellosus*) are here considered synonyms of *P. flavicornis*. One of the remaining names refers to an apparently distinct species (*P. veneficus* Wheeler), while the others are synonyms of *P. ferrugineus* (*q.v.*). The worker of *P. flavicornis* is distinguished from other obligate acacia-ants (*P. ferrugineus* group) by its dark brown or black color (mesosoma sometimes contrastingly lighter); broad, densely punctate, opaque head which lacks a sublucid area posteromesad of the compound eye (in contrast to *P. ferrugineus*); and narrow, anteroventrally subtended, median clypeal lobe, whose lateral corners are rounded.

Pseudomyrmex gracilis (Fabricius)

Formica gracilis Fabricius, 1804:405. Syntype worker, Essequibo, Guyana (Smidt) (ZMUC) [Examined]; here designated LECTOTYPE.

Pseudomyrma variabilis F. Smith, 1877:62. Syntype worker, "Barbadoes" (BMNH) [Examined]; here designated LECTOTYPE. *Syn. nov.*

The lectotype worker of *P. gracilis*, although lacking a head, seems to correspond rather well to the concept of *P. gracilis* which has become prevalent in publications. The mesosoma, postpetiole, and gaster are dark brown to black, the petiole a contrasting light castaneous brown; fine, silvery (not black) pilosity covers most of the body, and the associated piligerous punctures subdue the lustre of the integument; the petiole is narrow and slender, with a long anterior peduncle; and the pronotum is margined laterally but not sharply so. I do not attach much taxonomic significance to the light-colored petiole. The *P. gracilis* lectotype worker agrees well with material from Kartabo, Guyana (leg. Wheeler) in which there is variable infuscation of the petiole. A second worker in the *P. gracilis* "type series" in ZMUC, with a red "TYPE" label, but no locality or identification label, is in fact not conspecific (it is a worker of *P. maculatus* (F. Smith)) and should be excluded from consideration as type.

There is a bewildering and variable array of forms, variously described as subspecies or "varieties" of *P. gracilis*, which require detailed taxonomic study. I suspect that most of these will prove to be synonyms of a single polytypic species (*P. gracilis*), but at this stage there is insufficient information about the intra- and inter-specific components of this variation. One unambiguous synonymy can be established here: the lectotype worker of *P. variabilis* (F. Smith) in BMNH agrees very closely with that of *P. gracilis*, the only substantial difference being that the *P.*

variabilis petiole is black. I have designated a lectotype of *P. variabilis* because a second worker glued to the same card (and bearing therefore the same type label as *P. variabilis*) is that of a different species – *P. maculatus* (F. Smith)! I have printed a lectotype label for *P. variabilis* and marked the card shared by the two specimens in such a way that the *P. maculatus* worker is clearly excluded as a type specimen of *P. variabilis*.

Pseudomyrmex holmgreni (Wheeler)

Pseudomyrma holmgreni Wheeler, 1925:11. Two syntype workers, Chaquimayo, Peru (N. Holmgren) (NHRS) [Examined]. One worker here designated LECTOTYPE.

Contrary to statements in the original description, this widespread South American species is not closely related to *P. filiformis*. Rather, it is a member of the *P. pallidus* group, bearing some resemblance to *P. euryblemma* (*q.v.*) but differing in the following worker characters: metanotal groove wider and more deeply incised; basal face of propodeum subequal in length to declivitous face (longer than the declivitous face in *P. euryblemma*); and head tending to be more elongate, with the sides rounding more gradually into the occipital margin. The workers and queens of *P. holmgreni* vary considerably in color, from concolorous orange to dark brown, including intermediate forms with variable degrees of infuscation of the body.

Pseudomyrmex laevifrons Ward, *nom. nov.*

Pseudomyrma laeviceps F. Smith, 1877:63. Two syntype workers, Para, Brazil (BMNH) [Examined]. One syntype worker here designated LECTOTYPE. [Preoccupied by *Pseudomyrma laeviceps* F. Smith, 1859 = *Tetraponera laeviceps* (F. Smith)].

This is a small (worker HW 0.48–0.56, n=14) distinctive species with closely contiguous, anterodorsally elevated frontal carinae; a smooth, shiny, puncticulate head; long eyes; and, in the workers, an unusually shaped propodeum such that the basal and declivitous faces meet at a sharp angle. The known range of *P. laevifrons* extends from Costa Rica to Bolivia and Brazil.

Pseudomyrmex malignus (Wheeler)
(Figure 41)

Pseudomyrma maligna Wheeler, 1921b:143. Syntype workers, males, queens, Kartabo, Guyana (W.M. Wheeler) (MCZC, MZSP) [Examined].

Pseudomyrma maligna var. *cholerica* Wheeler, 1921b:146. Syntype workers, Kartabo, Guyana (W.M. Wheeler) (MCZC) [Examined] *Syn. nov.*

Pseudomyrma maligna var. *crucians* Wheeler, 1921b:147. Syntype workers, Kartabo, Guyana (W.M. Wheeler) (MCZC) [Examined] *Syn. nov.*

Pseudomyrma auripes Wheeler, 1922:5. Holotype queen, Trinidad, July 1920 (W.M. Wheeler) (MCZC) [Examined] *Syn. nov.*

Workers and queens of this *Tachigali*-associated ant species are distinguished from those of *P. concolor* (= *P. latinodus*) by the following features: median clypeal lobe less ventrally deflected, laterally subangulate (Fig. 41); erect pilosity sparser, lacking on sides of head above the eyes (frontal view); and anteroventral process of petiole more prominently recurved, hook-like. In addition, the queen has distinctive, basally geniculate mandibles (*e.g.,* Wheeler, 1921b, Fig. 14). The color and size variation reflected in the "varieties" *cholericus* and *crucians* can be seen within single nest series.

See also the discussion under *P. concolor* and *P. tachigaliae* (Forel).

Pseudomyrmex osurus (Forel), *stat. reval.*

Pseudomyrma levigata [sic] subsp. *osura* Forel, 1911:279. Syntype worker, Costa Rica (Pittier) (MHNG) [Examined]. *Stat. reval.* [Incorrectly synonymized (provisionally) under *P. faber* (F. Smith) by Kempf, 1958:449].

Pseudomyrma laevigata subsp. *insularis* Enzmann, 1945:88. Holotype worker, Barro Colorado Island, Panama (location unknown) [not examined]. *Syn. nov.* [Incorrectly synonymized (provisionally) under *P. faber* (F. Smith) by Kempf, 1958:449].

Examination of the syntype worker of *P. osurus* shows this to be a distinct species, differing from *P. faber* (F. Smith) by the shape of the petiole (possessing a distinct anterior peduncle and differentiated node, in lateral view), and the smooth, shiny puncticulate head. Enzmann's description of *P. insularis* fits *P. osurus* tolerably well, and agrees more closely with *P. osurus* than with any other species in the *P. laevigatus* complex known to me from Central America.

P. osurus is typically concolorous orange (head black in some Costa Rican and Colombian workers, which I take to be this species), while *P. faber* is more variable, with some workers (including the type) having a dark brown to black head and mesosoma.

Pseudomyrmex pazosi (Santschi), *stat. nov.*

Pseudomyrma pazosi Santschi, 1909:309. Syntype workers, queens, Cuba (Pazosi) (NHMB) [Examined]. One syntype worker here designated LECTOTYPE.

Pseudomyrma flavidula var. *pazosi* Santschi; Wheeler, 1913:484.

Pseudomyrma flavidula var. *jaumei* Aguayo, 1932:217. Holotype worker, El Palenque, Cuba (M. Jaume) (MCZ) [Examined] *Syn. nov.*

P. pazosi is a small (worker HW < 0.76) Cuban species in the *P. pallidus* group, with orange head, mesosoma, petiole, and postpetiole, and a contrasting black gaster; smooth, shiny puncticulate head; broad fore femur; and a gaster devoid of dense pubescence. The *P. jaumei* holotype merely represents a faded, discolored *P. pazosi* worker.

Pseudomyrmex perboscii (Guérin)
(Figure 43)

Myrmex perboscii Guérin, 1844:428. Holotype queen, Baie de Campeche, Mexico (Perbosc) (not in MCSN, MNHN, or ZSMC) [Not examined].

Tetraponera testacea F. Smith, 1852:45. Holotype dealate queen, [Rio] Napo, Peru (BMNH) [Examined] *Syn. nov.*

Pseudomyrma perbosci [sic] Guérin; Forel, 1899:96 [Description of worker].

Pseudomyrma simoides Forel, 1911:281. Syntype worker, Amazonas, Brazil (Bates) (MHNG) [Examined] *Syn. nov.*

Pseudomyrma icterica Wheeler, 1922:4. Holotype worker, Port of Spain, Trinidad (A. Busck) (MCZC) [Examined] *Syn. nov.*

This medium-sized species (worker HW 1.09–1.44, n=15) has a truncate median clypeal lobe, which is sharply rounded laterally (Fig. 43); relatively well-separated frontal carinae (MFC subequal to distal scape width) and conspicuously protruding median lobes of the antennal sclerites; a deeply incised metanotal groove (in the worker); and a somewhat shiny, orange- to testaceous-brown, integument, the gaster sometimes darker in color. The head and mesosoma have fine, punticulate sculpture, the punctulae varying in density, as do the minute, piligerous punctures (and associated appressed pubescence) on the postpetiole and gaster. Standing pilosity is fine and rather sparse (lacking on outer faces of the tibiae and on the worker mesonotum).

Having examined the types of *P. testaceus*, *P. simoides*, and *P. ictericus*, I feel fairly confident about the specific identity of these three. Moreover, they appear to be conspecific with the "*Pseudomyrma perbosci*" worker described by Forel (1899) from Costa Rica. Unfortunately, the type of *P. perboscii* could not be located, but the original description, while scanty, contains enough information to justify the above synonymy. Among the features mentioned by Guérin, the combination of the elongate, subrectangular head (nearly twice as long as wide), globose postpetiole, fawn-yellow body with dark gaster, finely shagreened to shiny appearance, and large size (9.5mm long), fits the queen of no other species known to me.

In northern Colombia and Venezuela I collected colonies of this species in live terminal branches of saman (*Pithecellobium saman*) trees. The ants occupied numerous unconnected cavities, 5–20 mm long (2–4 mm internal diameter) in which they kept brood and tended coccids. The cavities appeared to be intrinsic to the plant since unoccupied cavities, without entrance holes, could be found. Although the workers patrolled the foliage and would sting if molested, they were much less aggressive than the *Pseudomyrmex* ants inhabiting *Tachigali*, *Triplaris*, or swollen-thorn acacias. Thus the association may represent an early (or arrested?) phase in the development of an ant-plant mutualism.

Pseudomyrmex rufiventris (Forel) *stat. nov.*

Pseudomyrma kurokii var. *rufiventris* Forel, 1911:275. Syntype queen, San Bernardino, Paraguay (K. Fiebrig) (ZSMC) [Examined].

Although obviously closely related to *P. euryblemma* (= *P. kurokii*) (*q.v.*), *P. rufiventris* appears to be distinct enough to warrant specific status. The head of the queen and worker is covered with dense, punctulate-coriarious sculpture which renders it opaque; this may be contrasted with a weaker puncticulate sculpture and sublucid appearance in *P. euryblemma*.

Pseudomyrmex rufomedius (F. Smith)

Pseudomyrma rufomedia F. Smith, 1877:66. Syntype alate queen (unique), Aceituno, Guatemala (BMNH) [Examined].

Pseudomyrma stolli Forel, 1912:20. Syntype worker, queens, male, Retalhuleu, Guatemala (Stoll)(MHNG) [Examined] *Syn. nov.*

P. rufomedius is a distinctive species, known only from Guatemala and southern Mexico, workers and queens of which possess a broad head with relatively small eyes; a flattened and laterally marginate pronotum; a more or less apendunculate petiole, much longer than high or wide, whose dorsal face is also flattened and laterally margined; very fine, pale, inconspicuous pilosity; and a bicolored body (orange petiole contrasting with dark brown head and gaster; remainder of body variably infuscated). An additional characteristic feature of the worker is the virtual obliteration of the metanotal groove, the mesonotum and propodeum forming a continuous, elevated, and laterally compressed plate.

The *P. rufomedius* type, although lacking a head, agrees closely with the worker-associated queens of *P. stolli* (and other material which I have examined), and there can be no doubt about the identity of the species (*cf.* Perrault, 1987).

Pseudomyrmex simplex (F. Smith)

In reviewing this species, as one of these occurring in the Nearctic region, I interpreted incorrectly the type locality "St. Paul" to be in the state of São Paulo, Brazil (Ward, 1985:238). In fact, "St. Paul" refers to São Paulo de Olivença, a Bates collecting locality in the Brazilian state of Amazonas (Kempf, 1972).

Pseudomyrmex spinicola (Emery)
(Figure 44)

Pseudomyrma spinicola Emery, 1890:64. Syntype workers, queens, males, Alajuela, Costa Rica (Alfaro) (MCSN) [Examined]. One worker here designated LECTOTYPE.

P. spinicola is a common species of acacia–ant, ranging from Honduras to Colombia, workers of which are distinguished from those of the more northerly species, *P. ferrugineus*, by the following traits: median clypeal lobe with a concave anterior margin and with lateral angles or teeth (Fig. 44); frontal carinae more closely contiguous and median lobes of antennal sclerites correspondingly more exposed; frons with more extensive shiny interspaces between the punctures;

propodeal spiracles more salient in dorsal view; petiole longer, with a tendency towards more pronounced posterolateral angles in dorsal view.

Most of the forms described as subspecies or varieties of *P. spinicola* are probably conspecific with it (with the exception of *P. convarians* (Forel)), but I refrain from proposing formal synonymy until the variation is better understood.

<p style="text-align:center">*Pseudomyrmex tachigaliae* (Forel) *stat. nov.*
(Figure 42)</p>

Pseudomyrma latinoda race *tachigaliae* Forel, 1904b:686. Syntype workers, queens, males, Tarapoto, Peru (Ule) (MHNG) [Examined].

Pseudomyrma latinoda subsp. *bradleyi* Wheeler, 1942:169. Syntype workers, Perene, Peru (Bradley) (MCZC) [Examined] *Syn. nov.*

Pseudomyrma bradleyi Enzmann, 1945:82. Syntype workers, Perene, Peru (Bradley) (MCZC) [Examined] [Objective synonym of *Pseudomyrma latinoda bradleyi* Wheeler; Brown, 1949:42]

This *Tachigali*-ant is apparently confined to the western Amazon basin and adjacent foothills. The worker is recognized by the laterally angulate and inflected median clypeal lobe (Fig. 42); subcontiguous frontal carinae (MFC < basal scape width); sparse and inconspicuous pilosity; and dense appressed pubescence which is much better developed than in *P. malignus* or *P. concolor*.

<p style="text-align:center">*Pseudomyrmex tenuis* (Fabricius)</p>

Formica tenuis Fabricius, 1804:405. Syntype worker, Essequibo, Guyana (Smidt) (ZMUC) [Examined]; here designated LECTOTYPE.

The lectotype worker of *P. tenuis* is concolorous testaceous brown, with a densely punctate, opaque head; large elongate eyes; inflected, tectiform median clypeal lobe; sharply margined pronotum; tall, thin, anterodorsally angulate (pointed) petiole; and no erect pilosity on the mesosoma dorsum. This agrees with the concept of *P. tenuis* which has been prevalent in the literature.

For a listing of synonyms see Kempf (1972), but note that *P. nigriceps* (F. Smith) is now a junior synonym of *P. termitarius* (F. Smith) (Perrault, 1987).

<p style="text-align:center">*Pseudomyrmex triplaridis* (Forel)</p>

Pseudomyrma triplaridis Forel, 1904b:684. Syntype workers, queens, male, Jurua Miry, Jurua, Amazonas, Brazil (Ule) (MHNG) [Examined].

Pseudomyrma triplaridis subsp. *boxi* Wheeler, 1942:184. Syntype workers, queens, males, Blairmont, Berbice, Guyana (H.E. Box) (MCZC) [Examined] *Syn. nov.* One syntype worker here designated LECTOTYPE.

The worker of this *Triplaris*-associated ant has a sublucid, densely punctate head which is distinctly broader than that of *P. viduus* (CI 0.87–0.93, n=17); frontal carinae more closely contiguous than in *P. triplarinus* or *P. dendroicus* but less so than in *P. viduus* (FCI 0.071–0.109); a median clypeal lobe which is sharply rounded laterally; and a conspicuous, recurved (hook-like) subpetiolar process.

I have designated a lectotype of *P. boxi* because the type series in the MCZC contains a few workers of *P. viduus* (*q.v.*). Wheeler (1942) confused these two species; the main series of *P. viduus* from Blairmont, Guyana was described by him as a second subspecies of *P. triplaridis* (*P. triplaridis tigrinus*).

Pseudomyrmex viduus (F. Smith)

Pseudomyrma vidua F. Smith, 1858:158. Syntype male (unique), Ega, Amazonas, Brazil (BMNH) [Examined].

Pseudomyrma caroli Forel, 1899:89. Syntype workers, queens, Nicoya, Costa Rica (M. R. Alfaro) (MCSN, MHNG) [Examined]. *Syn. nov.*

Pseudomyrma caroli var. *sapii* Forel, 1904b:688. Syntype workers, queens, Bom Fim, Jurua, Amazonas, Brazil (Ule) (MHNG) [Examined]. *Syn. nov.*

Pseudomyrma ulei Forel, 1904b:689. Syntype workers, queens, Jurua Miry, Jurua, Amazonas, Brazil (Ule) (MHNG) [Examined]. *Syn. nov.*

Pseudomyrma triplaridis subsp. *baileyi* Wheeler, 1942:185. Syntype workers, queens, Camaria, Cuyuni River, Guyana (W. M. Wheeler) (MCZC) [Examined] *Syn. nov.*

Pseudomyrma triplaridis subsp. *tigrina* Wheeler, 1942:186. Syntype workers, males, Blairmont, Berbice, Guyana (H. E. Box) (MCZC) [Examined] *Syn. nov.* One syntype worker here designated LECTOTYPE.

Pseudomyrma triplaridis subsp. *biolleyi* Enzmann, 1945:93. Syntype workers, queens, Camaria, Cuyuni River, Guyana (W. M. Wheeler) (MCZC) [Examined] [Objective synonym of *P. triplaridis baileyi* Wheeler; Brown, 1949:43].

Pseudomyrma triplaridis subsp. *trigona* Enzmann, 1945:94. Syntype workers, males, Blairmont, Berbice, Guyana (N. E. Box) (MCZC) [Examined] [Objective synonym of *P. triplaridis tigrina* Wheeler; Brown, 1949:43].

The type of *P. viduus* is a damaged male lacking head, postpetiole, and gaster. Nevertheless the shape of the petiole (in particular, the broad anterior peduncle; MPW = 0.22, PWI3 = 0.61) and general habitus clearly place it in the cluster of species which Kempf (1961) called the *P. latinodus* group (*cf.* Perrault, 1987). I compared it with males of likely candidate species, namely *P. concolor* (= *P. latinodus*), *P. nigrescens, P. tachigaliae, P. malignus, P. caroli, P. triplaridis, P. symbioticus, P. triplarinus,* and *P. dendroicus.* The *P. viduus* type agrees closely with males of *P. caroli* with respect to size, pilosity, mesonotal sculpture, and (especially) shape of the petiole, while disagreeing with the remaining species in petiole shape and in one or more aspects of size, pilosity, or sculpture. Specifically, *P. viduus* has a shiny punctate mesonotum, covered with both appressed pubescence and fine, golden pilosity, the latter up to 0.20 mm long; conspicuous pilosity on the legs and petiole (*ca.* 19 standing hairs in outline on the petiolar dorsum); an elongate petiole (PLI = 0.52); and small absolute size (PL = 0.77, PH = 0.40, DPW = 0.36, mesonotal width = 0.92). Only males of *P. caroli* agree with this combination of characters. The other names listed under the synonymy of *P. viduus* (*P. sapii, P. ulei P. baileyi, P. tigrinus*, and Enzmann's copycat names) appear to represent nothing more than the normal variation of the species heretofore known as *P. caroli.* Workers and queens of this species can be recognized by their elongate heads (worker CI 0.70 – 0.80, n=22; queen CI 0.62 – 0.68, n=8) and closely adjacent frontal carinae (worker FCI 0.048 – 0.087; queen FCI 0.062 – 0.085) compared to

other members of the erstwhile *P. latinodus* group (here referred to as the *P. viduus* group).

As I presently understand it, *P. viduus* is a widespread, somewhat variable species, and a generalist occupant of ant-plants. Colonies have been collected within live branches or cavities of *Ocotea, Cordia, Sapium, Coussapoa*, and *Triplaris*. Detailed biological studies of *P. viduus* may reveal several cryptic species, associated with particular ant-plants, but the present material does not support any clear division(s).

Summary of Taxonomic Changes

P. concolor (F. Smith), 1860.
    = *P. latinodus* (Mayr, 1877), *syn. nov.*
P. dendroicus (Forel, 1904a), *stat. reval.*
    = *P. emarginatus* (Forel, 1904b), *syn. nov.*
P. ejectus (F. Smith, 1858).
    = *P. lincecumii* (Buckley, 1866), syn. nov.
P. euryblemma (Forel, 1899).
    = *P. kurokii* (Forel, 1906), *syn. nov.*
P. ferrugineus (F. Smith, 1877).
    = *P. fulvescens* (Emery, 1890), *syn. nov.*
    = *P. canescens* (Wasmann, 1915), *syn. nov.* (preoccupied)
    = *P. wasmanni* (Wheeler, 1921a) (replacement name for *P. canescens* Wasmann).
    = *P. bequaerti* (Wheeler, 1942), *syn. nov.*
    = *P. saffordi* (Wheeler, 1942), *syn. nov.*
    = *P. vesanus* (Wheeler, 1942), *syn. nov.*
    = *P. honduranus* (Enzmann, 1945), *syn. nov.*
P. filiformis (Fabricius, 1804).
    = *P. longiceps* (Forel, 1906), *syn. nov.*
    = *P. longiceps* (Stitz, 1933), *syn. nov.* (preoccupied).
P. flavicornis (F. Smith, 1877).
    = *P. belti* (Emery, 1890), *syn. nov.*
    = *P. obnubilus* (Menozzi, 1927), *syn. nov.*
    = *P. fellosus* (Wheeler, 1942), *syn. nov.*
P. gracilis (Fabricius, 1804).
    = *P. variabilis* (F. Smith, 1877), *syn. nov.*
P. holmgreni (Wheeler). No taxonomic changes proposed.
P. laevifrons Ward, *nom. nov.*
    = *P. laeviceps* (F. Smith, 1877) (preoccupied).
P. malignus (Wheeler, 1921b).
    = *P. cholericus* (Wheeler, 1921b), *syn. nov.*

= *P. crucians (Wheeler, 1921b), syn. nov.*

= *P. auripes* (Wheeler, 1922), *syn. nov.*

P. osurus (Forel, 1911), *stat. reval.*

= *P. insularis* (Enzmann, 1945), *syn. nov.*

P. pazosi (Santschi, 1909), *stat. nov.*

= *P. jaumei* (Aguayo, 1932), *syn. nov.*

P. perboscii (Guérin, 1844).

= *P. testaceus* (F. Smith, 1852), *syn. nov.*

= *P. simoides* (Forel, 1911), *syn. nov.*

= *P. ictericus* (Wheeler, 1922), *syn. nov.*

P. rufiventris (Forel, 1911), *stat. nov.*

P. rufomedius (F. Smith, 1877).

= *P. stolli* (Forel, 1912), *syn. nov.*

P. simplex (F. Smith). No taxonomic changes proposed.

P. spinicola (Emery). No taxonomic changes proposed.

P. tachigaliae (Forel, 1904b), *stat. nov.*

= *P. bradleyi* (Wheeler, 1942), *syn. nov.*

P. tenuis (Fabricius). No taxonomic changes proposed.

P. triplaridis (Forel, 1904b).

= *P. boxi* (Wheeler, 1942), *syn. nov.*

P. viduus (F. Smith, 1858).

= *P. caroli* (Forel, 1899), *syn. nov.*

= *P. sapii* (Forel, 1904b), *syn. nov.*

= *P. ulei* (Forel, 1904b), *syn. nov.*

= *P. baileyi* (Wheeler, 1942), *syn. nov.*

= *P. tigrinus* (Wheeler, 1942), *syn. nov.*

CONCLUDING REMARKS

The taxonomic findings presented in this paper illustrate two recurring patterns in the genus *Pseudomyrmex*: the occurrence of closely related (sibling) species with broadly overlapping geographical ranges and, at the same time (if my interpretation of synonymy is correct), the existence of considerable geographical variation *within* many species.

There are relatively few allopatric pairs of sister species in the genus (*P. curacaensis* and *P. cretus* are one possible example). *Pseudomyrmex* queens of all species are fully winged and capable of dispersal; such vagility may be responsible for the relative rapidity with which recently speciated forms come into secondary contact (assuming that initial differentiation occurred in allopatry). Moreover, *Pseudomyrmex* species which are generalist nesters in dead twigs – and this is true of the majority of species – are remarkably tolerant of other congeners in the same habitat, with the result that allospecific colonies often share the same foraging space.

For example, thirteen species of *Pseudomyrmex* were observed foraging on the fig tree and adjacent vegetation, where the type specimens of *Pseudomyrmex spiculus* were collected.

Such close habitation is not typical of those *Pseudomyrmex* species which live in plant domatia. Colonies of these species seldom overlap in foraging space; yet there may be several species in a given locality. In the Tarapoto region of northern Peru, *Triplaris* plants are occupied by four related species in the *P. viduus* group; similar numbers of species co-occur on swollen thorn *Acacia in parts of Central America.*

The discrimination and identification of Pseudomyrmex species, which is generally feasible for sympatric collections, is made more difficult on a large geographical scale by the considerable variation which occurs within many taxa. This is hardly a novel situation – examples of polytypy are common in ants (Ward, 1989) – but the situation is aggravated in some *Pseudomyrmex* where the discriminatory value of characters varies from one region to another. Thus in Costa Rica, workers of *P. elongatus* and *P. caeciliae* are consistently separable on head sculpture, but in Guatemala and southern Mexico one encounters some individuals exhibiting intermediate conditions of this character. In western Mexico, where there appears to be a single taxon, which I take to be *P. elongatus*, individuals also tend to be shifted towards an intermediate condition. Similar situations occur in other species complexes. Whether the taxa concerned are truly discrete (but their identities obscured by character shifts in allopatry) or are in fact reproductively isolated in some regions but not others, cannot be determined without further population-level studies.

ACKNOWLEDGMENTS

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NOTE ADDED IN PROOF

Further study of Central American acacia-ants (*P. ferrugineus* group) permits recognition of the following species:

Pseudomyrmex peperi (Forel).

Pseudomyrma peperi Forel, 1913:213. Syntype workers, Patulul, Guatemala (Peper) (MHNG) [Examined].

Pseudomyrma spinicola race *convarians* Forel, 1913:214. Syntype worker, Patulul, Guatemala (Peper) (MHNG) [Examined] *Syn. nov.*

Pseudomyrma sabanica [sic] var. *saffirdi* Enzmann, 1945:89. Syntype workers, Yerba Santa, Chiapas, Mexco (G.N. Collins) (MCZC) [Examined] *Syn. nov.* [Incorrectly synonymized under *P. belti saffordi* (Wheeler) by Brown, 1949:42].

An obligate acacia-ant, distributed from southern Mexico to Nicaragua, *P. peperi* can be recognized by the following features in workers and queens: relatively small size (worker HW < 0.92, queen HW < 0.86); light to medium brown (not black)

coloration; densely punctulate, opaque head (presenting a matte appearance); and broad petiolar node with salient posterolateral angles.
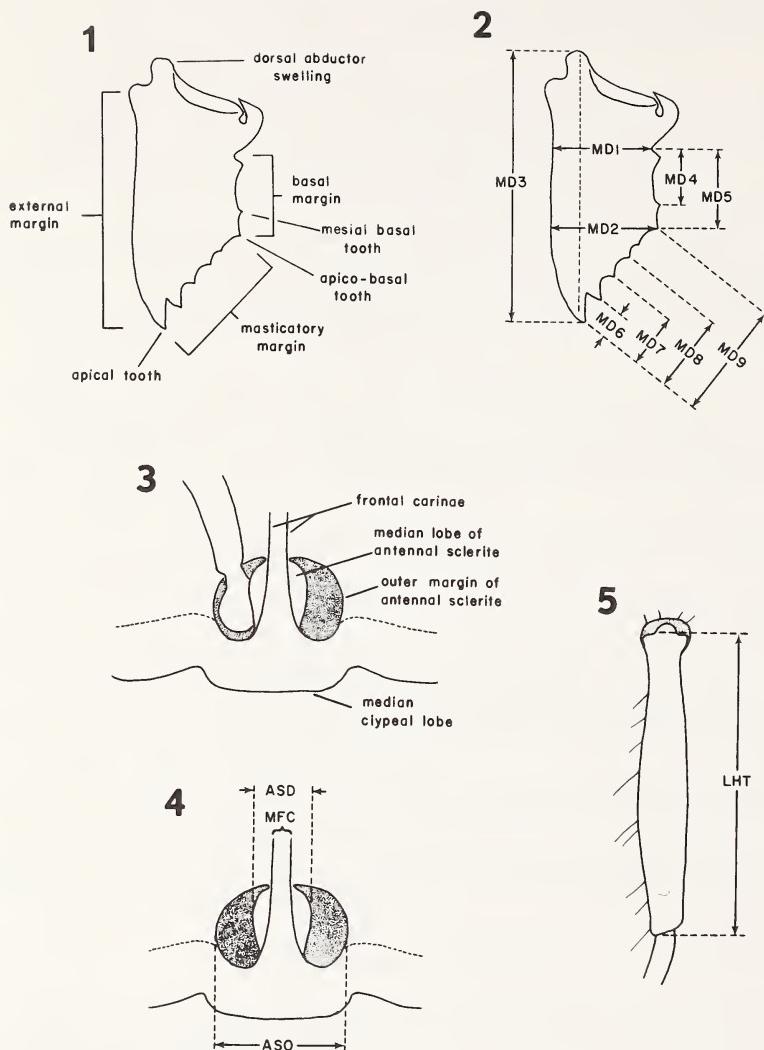
Figures 1–5. Illustrations of some measurements and morphological terms used for pseudomyrmecine ants (see also Figures 1–4 in Ward, 1985). Figs. 1, 2. *Pseudomyrmex* worker, right mandible: terminology and associated measurements. Figs. 3, 4. *Pseudomyrmex* worker, fronto-clypeal complex: terminology and associated measurements; right antenna (Fig. 3) and both antennae (Fig. 4) removed. Fig. 5. *Pseudomyrmex* worker, lateral view of left hind tibia, illustrating the measurement LHT.
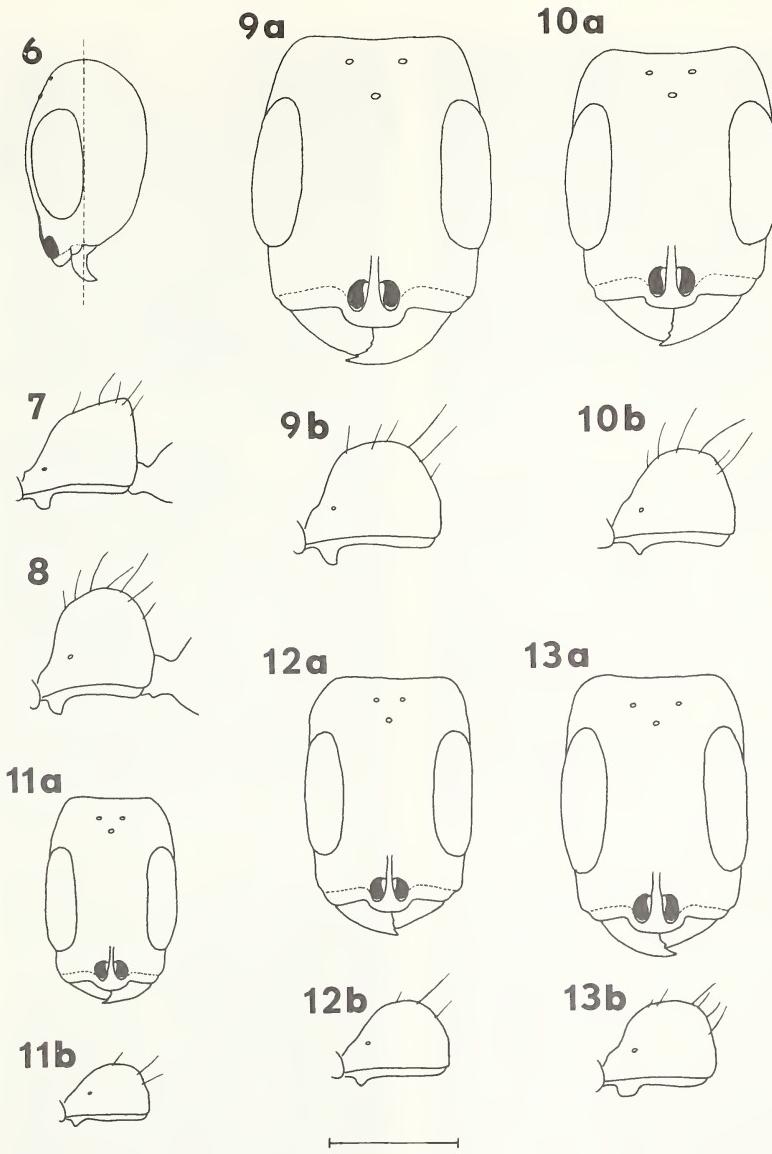
Figures 6–13. Various views of workers in the *Pseudomyrmex oculatus* group. Fig. 6. *P. elongatus*, lateral view of worker head, antennae removed, showing the plane of view utilized for a full-face, frontal (dorsal) view of head. Fig. 7. Lateral view of worker petiole, *P. oculatus* (Brazil). Fig. 8. Same, *P. schuppi* (Brazil). Figs. 9–13. Paired illustrations of head (frontal view) without antennae or pilosity and petiole (lateral view) of: *P. cretus*, holotype worker, Costa Rica (9a, 9b); *P. curacaensis*, worker, Colombia (10a, 10b); *P. pisinnus*, holotype worker, Brazil (11a, 11b); *P. urbanus*, worker, Brazil (12a, 12b); and *P. alustratus*, holotype worker, Peru (13a, 13b). All drawn to same scale; scale line = 0.5 mm.
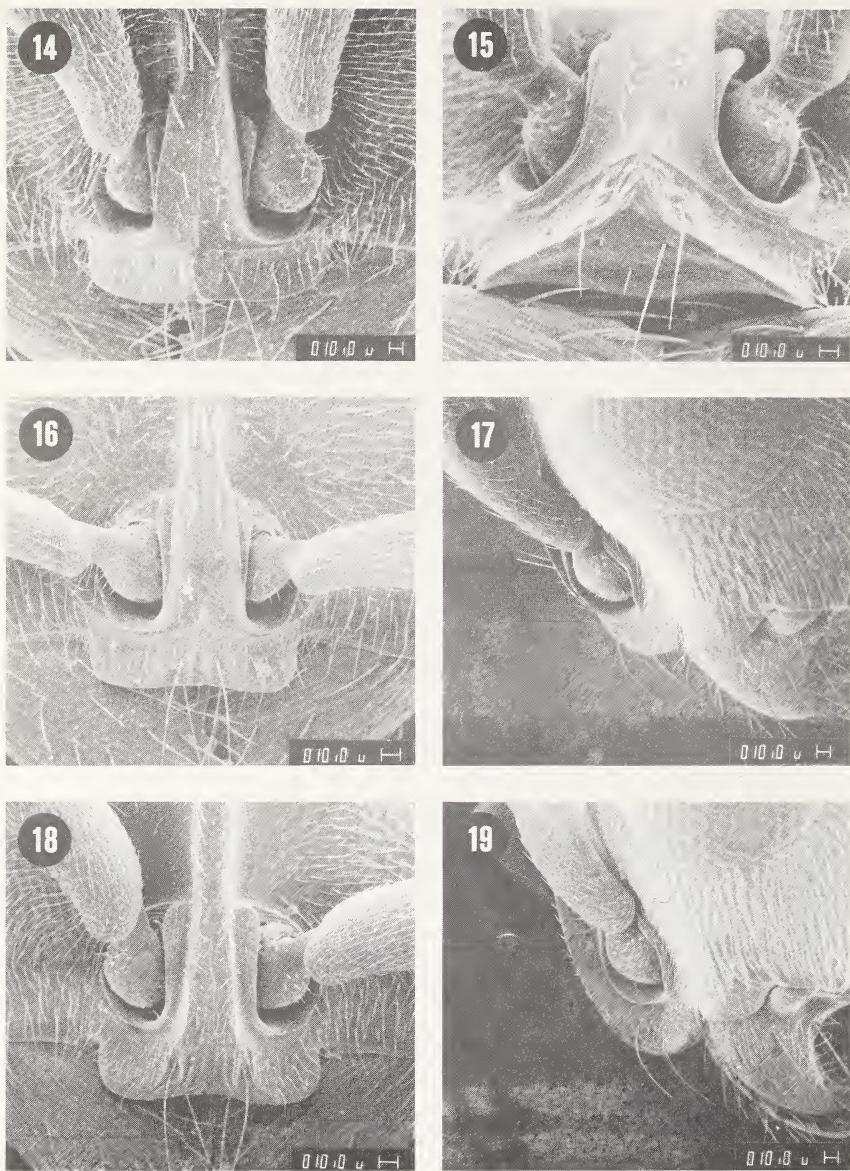
Figures 14–19. SEM views of the worker clypeus, in the *Pseudomyrmex oculatus* and *P. subtilissimus* groups. The "dorsal" views (figures 14, 16, 18) are taken perpendicular to the clypeus, and are thus "anterodorsal" relative to a full-face, dorsal view of the head (see figure 6). Fig. 14. *P. elongatus* (Mexico), dorsal view. Fig. 15. *P. elongatus* (Colombia), oblique anterior view. Fig. 16. *P. eduardi* (Venezuela), dorsal view. Fig. 17. *P. eduardi* (Venezuela), lateral view. Fig. 18. *P. tenuissimus* (Venezuela), dorsal view. Fig. 19. *P. tenuissimus* (Venezuela), lateral view.
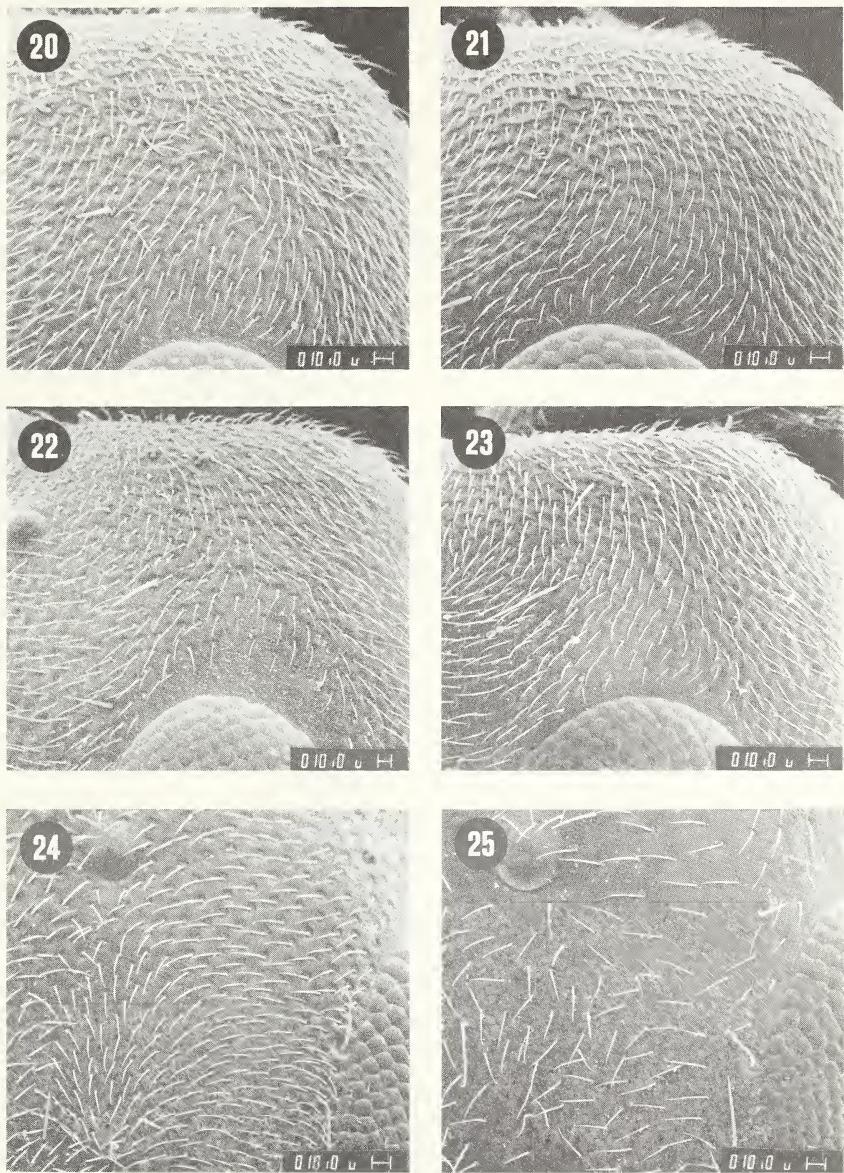
Figures 20–25. SEM views of worker head sculpture in the *Pseudomyrmex oculatus* group. Figs. 20–23. Supraocular sculpture: *P. elongatus*, Costa Rica (20); *P. elongatus*, Bolivia (21); *P. cubaensis*, Costa Rica (22); *P. caeciliae*, Guatemala (23). Fig. 24. Sculpture on left half of frons, *P. caeciliae*, Costa Rica. Fig. 25. Same, *P. eduardi*, Venezuela.
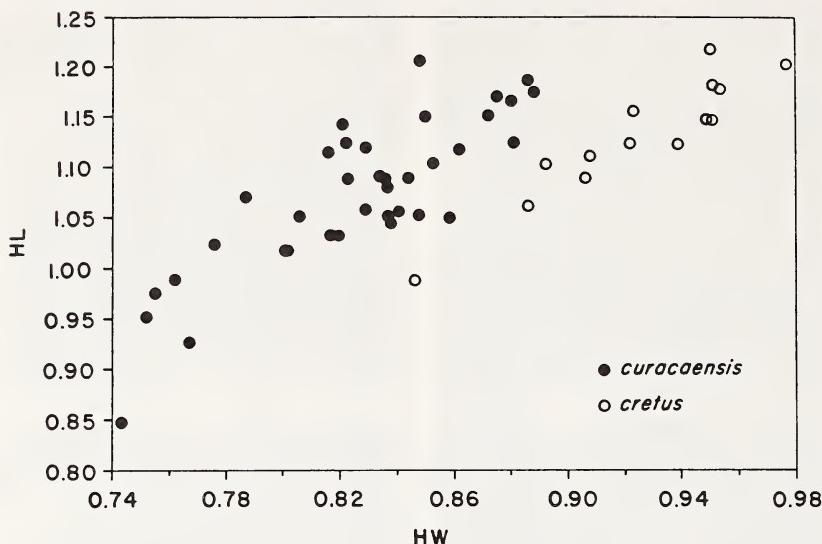
Figure 26. Scattergram of HL by HW, for workers of *Pseudomyrmex curacaensis* and *P. cretus*.
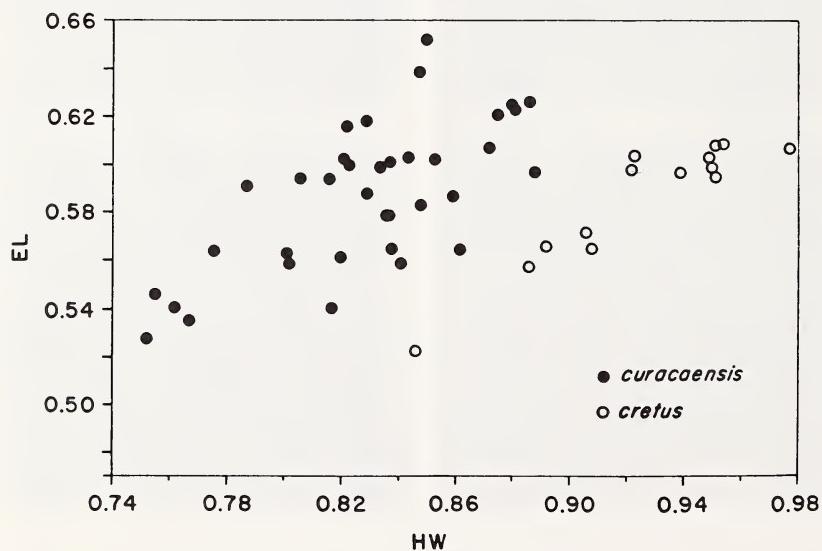
Figure 27. Scattergram of EL by HW, for workers of *P. curacaensis* and *P. cretus*.
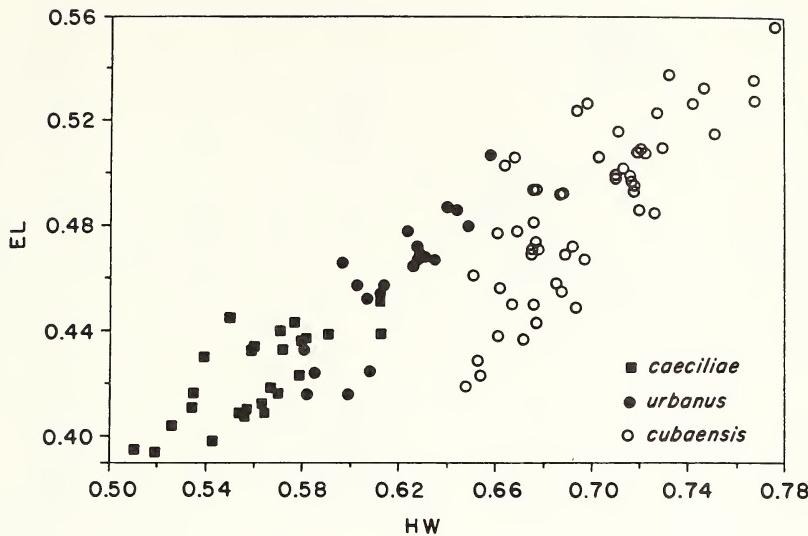
Figure 28. Scattergram of EL by HW, for workers of *P. caeciliae*, *P. urbanus*, and *P. cubaensis*.
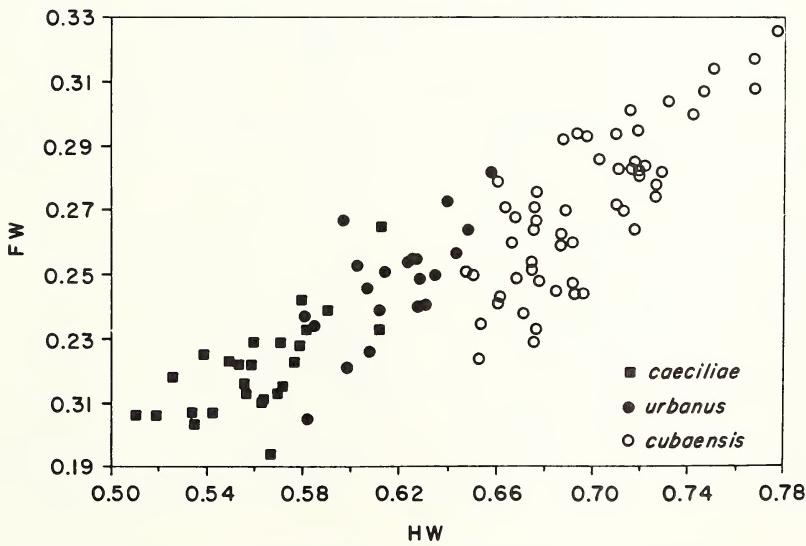
Figure 29. Scattergram of FW by HW, for workers of *P. caeciliae*, *P. urbanus* and *P. cubaensis*.
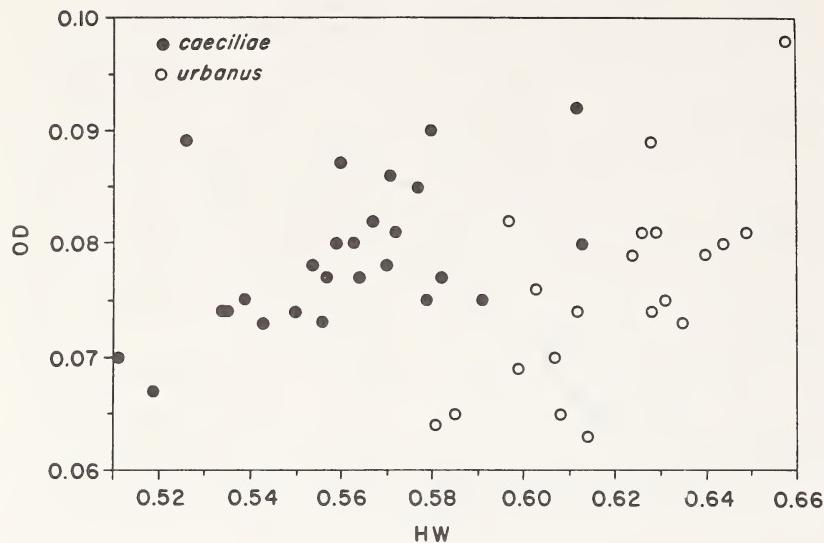
Figure 30. Scattergram of OD by HW, for workers of *P. caecil.ae* and *P. urbanus*. The two largest *P. caeciliae* workers come from Jamaica and are rather atypical.
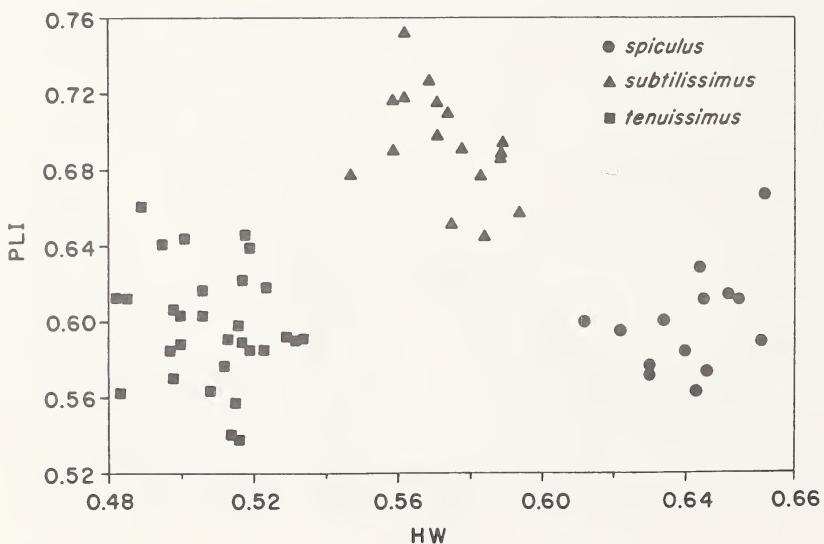
Figure 31. Scattergram of PLI (= PH/PL) by HW, for workers of *P. spiculus, P. subtilissimus,* and *P. tenuissimus.*
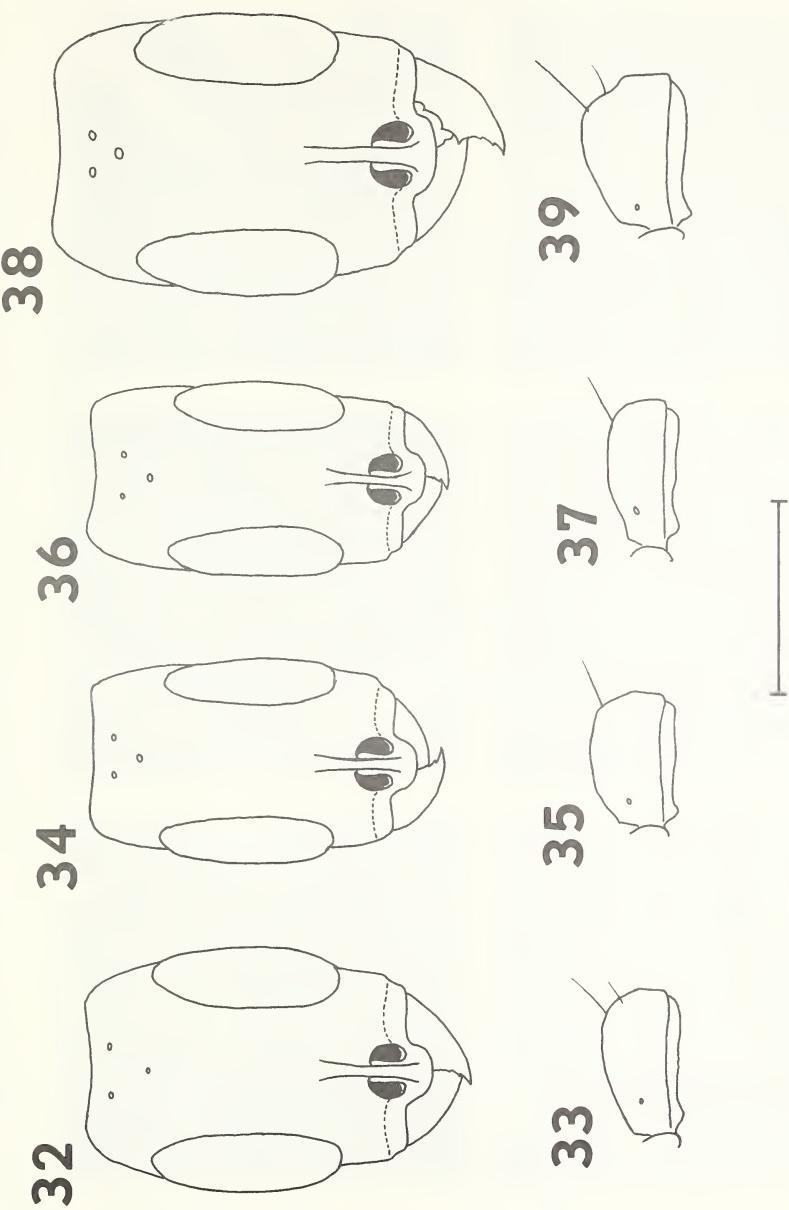
Figures 32–39. Paired illustrations of the head (frontal view) without antennae and petiole (lateral view) of workers in the *Pseudomyrmex subtilissimus* group: *P. spiculus*, holotype worker, Costa Rica (32, 33); *P. subtilissimus*, worker, Costa Rica (34, 35); *P. tenuissimus*, worker, Venezuela (36, 37); *P. villosus*, holotype worker, Brazil (38, 39). All drawings to same scale; scale line = 0.5 mm.
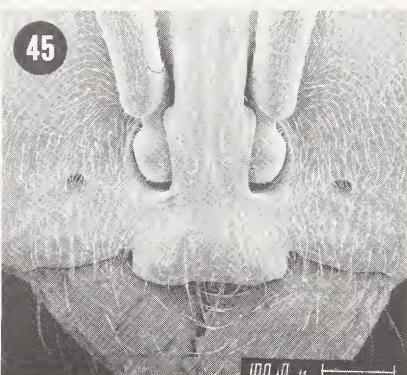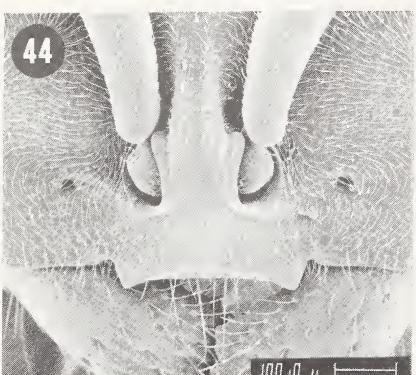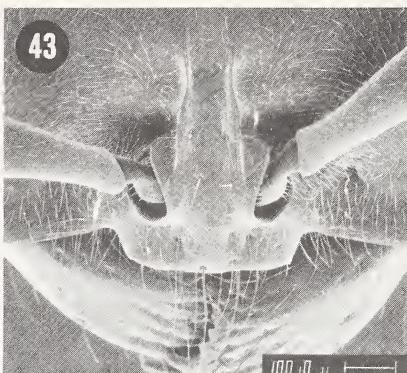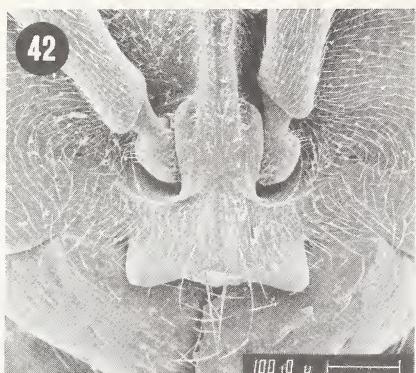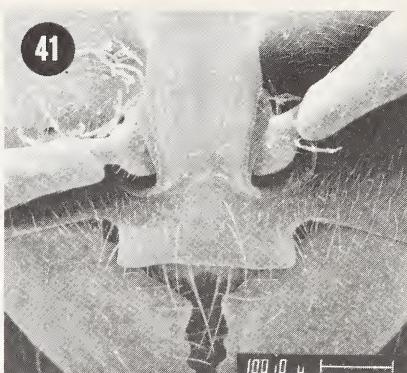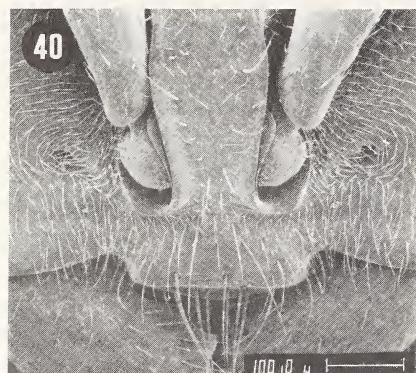
Figures 40–45. SEM views of the worker clypeus of various *Pseudomyrmex* species. These "dorsal" views are taken perpendicular to the clypeus, and are thus "anterodorsal" in relation to a full-face, dorsal view of the head (see figure 6). 40. *P. concolor*, Brazil. 41. *P. malignus*, Venezuela. 42. *P. tachigaliae*, Peru. 43. *P. perboscii*, Venezuela. 44. *P. spinicola*, Costa Rica. 45. *P. ferrugineus*, Mexico.

INDEX TO NAMES OF TAXA
(Junior synonyms in italics)

BOOK REVIEW

CAMPBELL, I., G. Theischinger & W.W.K. Houston, W.W.K. Houston & J.A.L. Watson, F.B. Michaelis & C.M. Yule, and A. Neboiss. 1988. Zoological Catalogue of Australia. Vol. 6. Ephemeroptera, Megaloptera, Odonata, Plecoptera, Trichoptera. Bureau of Flora & Fauna, Canberra. ed. W.W.K. Houston. Australian Government Publishing Service, GPO Box 84, Canberra, A.C.T. 2601. $Australian 29.95 (approx. $Canadian 27.00) incl. p. & p. ISBN 0 644 08269 3. xi+ 316 pp..

Not simply a list of names, synonymies, and literature associated with included taxa, this book includes notes on general distribution of species, and bibliographical annotations, where appropriate, by the authors of each ordinal section. Further, for each order, and family within orders, there is an introduction which includes comment on characteristics of the Australian fauna (endemism, *etc.*) of the taxon, a brief description of each life stage of the taxon, and brief notes on taxonomic history, biology, and distribution where available. The presentation, scope, and extent of the information thus provided varies between the orders included, depending, apparently, on the respective authors.

The orders are presented alphabetically, and the families within each are arranged, as the Preface puts it, "phylogenetically", whatever that may imply.

The genera, and species within genera are arranged alphabetically.

As the Preface points out, the nomenclature used for each taxon is governed by the 3rd (1985) edition of the International Code for Zoological Nomenclature.

The geographical area encompassed by the catalogue is outlined by the only illustration, a map of Australia and environs, on p. vi, and also by the Preface (p. vii) which names the offshore islands involved (including the Australian Antarctic Territory).

The Preface (incl. map) appears to be general for the series rather than specific to vol. 6. For example, that part which explains the format of the catalogue at the generic and specific levels employs an example from an obscure group of beetles, the Carabidae!

The format of presentation comprises 11 points as follows (abbreviated):

1. Genus valid name, author, year.
2. Genus available name, *etc.*, if any.
3. Qualifying statement, if any.
4. Type species, associated information.
5. Bibliographical references to synonymy.
6. Extralimital distribution.
7. Species valid name, author, year.
8. Species available name, *etc.*, if any.
9. Type data.
10. Distribution and ecology.

11.   Biological references (with brief notes on contents, as required, by the present authors).

Depending on the circumstances attendant on each taxon, some of the above points may be omitted.

The text, in common with other volumes of the series, is apparently generated from a computer file, which is being constantly updated. The implication appears to be that the next edition could appear 10 days after one acquires a current copy, or 10 years later. Indeed, this volume is so up to date that the existence of recognized but as-yet-undescribed species is mentioned in passing, in some instances.

The strictly catalogue portion of the text is followed by three appendices (I – Abbreviations and symbols; II – Museum acronyms; III – Taxonomic decisions made in this work) and five taxonomic indexes, one for each order treated, in which a species may be entered as many times as there are parts to the name (*e.g.,* a species will be entered under each of generic, subgeneric, and specific epithets, as appropriate).

Ordinal and familial introductions and references (which are given in full) are printed full page width, while generic and specific entries are in double columns.

As to the physical make-up of the book - the type face used is not easy on the eye; not restful. The only word which comes to mind is 'turgid'.

An oddity noted in passing is that, in the double column parts of the text, in order to avoid having a family entry ending half way down a column on the left or right of a page, the column will be split to give two parallel part columns, and the text suddenly changes from single to double spacing, with the words of the double spaced part-column themselves more widely spaced (the text margins are justified)! This practice occurs in various situations, not just the specific one above (*e.g.,* see pp. 217, 234).

The volume is printed on matt-finish, high quality paper, and amazingly, in these times, is strongly stitched in signatures. It won't fall apart in the hand! It is hard-bound in what appears to be a stout, institutional cloth. It's meant to last.

In closing, I mention a curiosity found on p. 178 (Trichoptera section). Neboiss writes "All publications containing original description have been sighted". Sighted?! I'm puzzled – does he mean cited; or seen? Is it merely a typographical error, or have these publications been granted the boon of vision?

For those who work on, and take more than a local approach to, any of the five orders included, this book is a must. At the price, it's a bargain.

Andrew P. Nimmo
Department of Entomology
The University of Alberta

BOOK NOTICE

NICHOLS, S. W. (compiler), and R. T. SCHUH (Managing Editor). 1989. The Torre-Bueno Glossary of Entomology. Revised Edition of a Glossary of Entomology by J. R. de la Torre-Bueno, including Supplement A, by George S. Tulloch. The New York Entomological Society and American Museum of Natural History. xvii + 840 pp. ISBN 0-913424-13-7. Price $35.00 U. S.

"**a-**, prefix; wanting or without (T-B; Harris)"; "**zymospecies-**, a species recognized soley [*sic*] on the basis of characters obtained through enzymes electrophoresis or comparable enzyme studies (Carlberg, pers. comm.)". These entries, respectively, begin and end the text of "The Torre-Bueno Glossary of Entomology".

Local entomological societies, at one time the backbone of entomology in North America, have been displaced somewhat from a focal role by national organizations. Nonetheless, their journals continue to provide outlets for first class publications, especially about systematics, morphology and ecology. In 1937, one such organization, the Brooklyn Entomological Society, published a work of inestimable value to entomologists and destined to become a classic: "A Glossary of Entomology", by J. R. de la Torre-Bueno. In the course of the next 50 years, copies of that publication, known to the initiated as simply "Torre-Bueno", appeared on the bookshelves of most North American entomologists, and on the bookshelves of entomologists from elsewhere who had occasion to read or write English entomological publications. As this work was becoming outdated, George S. Tulloch provided Supplement A, in 1962– but with the passage of time, that supplement became outdated, as well. Clearly, an extensive revision was required.

In the meantime, the Brooklyn Entomological Society and its assets became incorporated with the New York Entomological Society, the Executive of which determined to undertake a revision of the Torre-Bueno Glossary. Stephen W. Nichols was employed, and together with Randall T. Schuh of the American Museum, and some 50 editorial contributors, the work was undertaken, eventually leading to publication of a volume more than twice the size of the original "Torre-Bueno".

Prefatory material includes: a list of names of the Editorial Contributors; Table of Contents; Preface; Acknowledgements; Introduction to the Revised Glossary, to the Original Glossary, and to Supplement A; and a list of the 32 names of hexapod orders used in the Glossary. In the text, each main entry is in boldface type. For each entry, the authority or authorities who proposed it are cited.

Following the 823 pages of text, references are cited: "Principal Sources for the Current Edition"; "Additional Sources for the Current Edition"; "Non-English Language Glossaries and Sources"; "Sources to English Common Names of Insects"; and "Other Useful References".

A thick, heavy book, the volume has a strong binding of an attractive shade of brown buckram. Obviously, it is intended to last an entomologist for his working life. All in all, it is an aesthetically pleasing book, prepared with care and thought. This volume should be in the possession of every anglophone entomologist. At $35.00, it is the entomological buy of the latter half of the 20th Century.

The New York Entomological Society and American Museum of Natural History must be commended for undertaking publication of this volume. Those who worked to produce the text, and especially the compiler and the Managing Editor deserve high praise for their efforts. Perhaps in the fullness of time, entomologists will refer to this volume as their beloved "Nichols-Schuh", rather than "Torre-Bueno".

EDITOR'S ACKNOWLEDGEMENTS AND COMMENTS

Because of forgetfulness and the pressures associated with preparation for and departure on sabbatical leave, the Editor neglected to offer his thanks to those who assisted in evaluation and preparation of the contributions for Volume 24. Accordingly, the names of those who provided reviews for that volume are included in the following list. The able assistance, promptly and cheerfully rendered by all of the reviewers, is appreciated very much.

R. S. Anderson
    Department of Entomology, Texas A & M University
B. Bolton
    Department of Entomology, British Museum (Natural History)
T. L. Erwin
    Department of Entomology, U. S. National Museum of Natural History
R. H. Gooding
    Department of Entomology, University of Alberta
M. J. R. Hall
    Department of Entomology, British Museum (Natural History)
A. T. & H. F. Howden
    Department of Biology, Carleton University
D. H. Kavanaugh
    Department of Entomology, California Academy of Sciences
J. K. Liebherr
    Department of Entomology, Cornell University
M. W. Moffett
    Department of Entomology, Museum of Comparative Zoology, Harvard University
M. Sharkey
    Biosystematics Research Centre, Agriculture Canada
M. V. H. Wilson
    Department of Zoology, University of Alberta

During my absence, my colleague, Bruce S. Heming, acted as Editor. I am pleased to have this opportunity to thank him for his thorough and enthusiastic service.

French translations of abstracts were provided by J. C. Lacoursière, of my Department. J. S. Scott and D. Shpeley read proof, as requested, and assisted in other ways, as well.

The Publications Manager, Mrs. S. Subbarao, provided excellent service, both in production and in management of day-to-day operations of the office.

Our printers, Hallis Graphics Ltd., have served us well. I am mindful especially of prompt turnaround of our submissions, and the air of cordiality that characterizes our relationship with the President of Hallis, Mr. J. Haukedal.

With the publication of Volume 25, *Quaestiones Entomologicae* reached what is generally regarded as a landmark of some significance, and recognized as a Silver Anniversary. Although 25 years of publishing is an achievement, it seems sufficiently commonplace not to warrant a formal celebration. Such can be reserved for our 50th, or Golden Anniversary (in the year 2014), though the present members of the publications staff are unlikely to be in attendance.

In passing, I note that Volume 1 contains a paper by Richard Freitag, about tiger beetles, in the form of an analysis of the *Cicindela maritima* species group. Volume 25 contains a paper by the same author, about the Brazilian species of *Cicindela*. And in Volume 24, there is a paper by Timothy G. Spanton, about the species of the *Cicindela sylvatica* group, based on his Master's thesis - which was supervised by Freitag. Such connections through the passage of time indicate a stability that the Editor finds satisfying and gratifying.

It seems appropriate to offer a note of appreciation in memory of the late founder and first Editor of *Quaest. Ent.*, Brian Hocking, who died in 1974. In his introductory editorial, "words, words, words", Hocking noted the trend of marked increase in entomological publication, but saw it as the necessary consequence of burgeoning effort in research. Implicitly, he expressed dismay about: 1, "mounting page charges"; 2, the "publish or perish" blight; and 3, "the waning ability of administrators to judge publications by anything beyond their number". He recognized that points 2 and 3 were contributing, undesirably, to the marked increase in numbers of scientific publications.

He suggested that journals might help scientists keep abreast of the exponential increase in published information by ensuring presentation of more comprehensive papers ("It costs more in time, money, and effort to produce, file, store, retrieve, and read ten one page papers than one ten page paper"), to "index and abstract everything diversely", and to "make full use of modern techniques...even computers". *Quaest. Ent.* was organized along such lines.

Hocking paid tribute to entomology's "venerable indexing services" (Zoological Record; H. A. Hagen's Bibliotheca Entomologica; and W. Horn and S. Schenkling's Index Litteraturae Entomologicae). He held in high regard the contributions that such publications make to improve retrieval of entomological information.

At the time that he wrote, indexing and abstracting publications endeavoured to provide complete coverage of the entomological literature. This seems to be so no longer. The more blatantly commercial of such publications pick and choose which journals will be indexed or abstracted, and the status of journals in the scientific community now seems to be determined in part by whether or not their offerings are recorded by one or another commercial "service". Paralleling this development is the increasing trend of University administrators and granting agencies to evaluate

papers in terms of the journals in which they appear, rather than for their intrinsic merit. Many scientists have bowed to such pressure.

Thus, scientific publication now seems to have more to do with gaining individual recognition and prestige than with expressing desire to make known the results of research. Indeed, the medium is becoming the message. Perhaps it was ever thus, but Brian Hocking's generous spirit would be repelled by the mean, self-serving attitudes that have become commonplace in the scientific community. Such attitudes, of course, are simply latter-day expressions of the "publish or perish" syndrome that is a dark blight on the landscape of science.

Be that as it may, *Quaest. Ent.* has continued along the path that Hocking charted. The journal has kept its covenant with its founder as best it could - or so it seems to the present editor. Some subsequent Editor, who, metaphorically speaking, will blow out the candles on the journal's 50th Anniversary cake will be able to offer a more objective opinion than the one proffered by the present Editor, who has presided over this non-celebration of *Quaest. Ent.*'s 25th birthday.

George E. Ball
Editor